Eesti Maaülikool
Estonian University of Life Sciences

DISTURBANCE EFFECTS ON BOREAL FOREST ECOSYSTEM CARBON DYNAMICS

HÄIRINGUREŽIIMI MÕJU BOREAALSE METSAÖKOSÜSTEEMI SÜSINIKUVOOGUDELE

MEELIS SEEDRE

A Thesis
for applying for the degree of Doctor of Philosophy in Forestry

Väitekiri
filosoofiadoktori kraadi taotlemiseks metsanduse erialal

Tartu 2013

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, which are referred to in text by their Roman numerals.

I **Seedre, M.**, Shrestha, B.M., Chen, H.Y.H., Colombo, S. and Jõgiste, K. 2011. Carbon dynamics of North American boreal forest after stand replacing wildfire and clearcut logging. Journal of Forest Research 16, 168–183.

II **Seedre, M.**, and Chen, H.Y.H. 2010. Carbon dynamics of aboveground live vegetation of boreal mixedwoods after wildfire and clearcutting. Canadian Journal of Forest Research 40, 1862–1869.

III **Seedre, M.**, Taylor, A.R., Chen, H.Y.H. and Jõgiste, K. 2013. Dead wood density of five boreal tree species in relation to field assigned decay class. Forest Science 59, 261-266.

IV **Seedre, M.**, Taylor, A.R., Brassard, B.W., Chen, H.Y.H., and Jõgiste, K. (*Submitted to journal Ecosystems*). Total ecosystem carbon dynamics in young boreal forest: Comparison of wildfire and harvesting effects.

The contributions of the authors and other scientists to the papers:

	I	**II**	**III**	**IV**
Original idea	HC, **MS**	**MS**, HC	**MS**, HC	HC, AT, **MS**
Study design	**MS**	HC, **MS**	**MS**	HC, **MS**
Data collection	**MS**	**MS**	**MS**	**MS**, BB, BS, ZY, JL
Data analysis	**MS**	**MS**	**MS**, AT	**MS**
Manuscript preparation	**MS**, BS, HC, SC, KJ	**MS**, HC	**MS**, AT, HC, KJ	**MS**, AT, BB, HC, KJ

AT – Anthony Taylor, BB – Brian W. Brassard, BS – Bharat Shrestha, HC – Han Chen, JL – Jérôme Laganière, KJ – Kalev Jõgiste, **MS – Meelis Seedre**, SC – Steve Colombo, ZY – Zhiyou Yuan

ABBREVIATIONS

C	Carbon
D	Disturbance type
DBH	Breast height diameter
DW	Dead wood
DWD	Downed woody debris
FF	Forest floor
Ha	Hectare
Mg	Megagram (10^6 g)
Pg	Petagram (10^{15} g)
SOC	Soil organic carbon
TEC	Total ecosystem carbon
TSD	Time since disturbance
TSF	Time since fire

1. INTRODUCTION

Carbon (C) is a prominent chemical element playing an important part in earth's biogeochemical cycle (Pan *et al*., 2011). Terrestrial ecosystems store vast amounts of carbon and its interaction with the atmosphere has significant influence on global climate (Bonan, 2008). Accurate quantification of terrestrial C is needed for better understanding of biogeochemical cycles, for advancing our understanding of ecosystem function, and for validating soil-vegetation-atmosphere transfer models for better predictions of atmosphere biosphere interactions and climate (Krinner *et al*., 2005; Kull *et al.,* 2011; Stinson *et al*., 2011).

The boreal forest is one of the three major forest regions and forms a nearly contiguous circumpolar band in the northern hemisphere, occupying ca 14.7 million km^2 (Bonan and Shugart, 1989) and containing ca 66.7 Pg of C (Goodale *et al*., 2002). The boreal forest's large C stock is a result of long periods of light during the growing season and slow decomposition due to cold climate and poorly drained soils (Gower *et al*., 1997). Due to its size and high C content, it plays an important role in the global C cycle.

Carbon in forest ecosystems is located in four distinct pools that are different in their behaviour and functions, and interact during stand development when C is being allocated form one pool to another (Pregitzer and Euskirchen, 2004; **I**). Carbon from the atmosphere enters ecosystems through photosynthesis and is sequestered into live vegetation pool. When a plant dies C moves to the dead biomass pool, with fractions to the forest floor pool. Dead biomass (including belowground) and forest floor pool C slowly become incorporated into the mineral soil organic C pool. Throughout this process, C is also released to atmosphere via autotrophic and heterotrophic respiration.

Disturbances are important drivers of ecosystem processes. The type and frequency of disturbance largely determine forest ecosystem C amount and its dynamics (Banfield *et al*., 2002). Stand replacing disturbances restart forest development, and time since disturbance (TSD) is a primary indicator of current ecosystem state and its C balance (Brassard and Chen, 2006; Pregitzer and Euskirchen, 2004).

Historically fire has been the dominant disturbance in the boreal forest, but increasing demand for forest products has made harvesting a disturbance of significant importance (Kasischke *et al.*, 1995; Kurz and Apps, 1996; Weber and Flannigan, 1997). This shift in disturbance regimes has consequences on forest ecosystems that need to be understood as they can have significant effects on overall ecosystem function and therefore on global climate.

There are several other (stand replacing and non-stand replacing) natural disturbances with significant impacts to carbon dynamics (Fleming & Volney 1995; MacLean *et al.*, 2001). Disturbances like windthrow, insect and disease outbreaks, and flooding can strongly influence species composition, age structure, and stand dynamics, thus carbon storage and sequestration of forest ecosystems (MacLean *et al.*, 2001). Sometimes these disturbances can develop into large scale outbreaks like in western Canada where mountain pine beetle has caused enormous damage (Mathys *et al.*, 2013). However, in this thesis the dominant stand replacing disturbances (e.g. stand replacing fire and harvest) of boreal North American forests are studied.

2. REVIEW OF LITERATURE

2.1. Forest ecosystem carbon

Significant advances have been made in the study of forest ecosystem C and a robust understanding of the basic processes of C dynamics exists (Goetz *et al.*, 2012; Pregitzer and Euskirchen, 2004; **I**). Live biomass has been studied by Gower *et al.* (1997) and in study **II**, dead wood by Brassard and Chen (2008) and Boulanger and Sirois (2006), the forest floor by Shrestha and Chen (2010) and Rapalee *et al.* (1998) and mineral soil by Chen and Shrestha (2012) and Laganière *et al.* (2013). Few have also quantified all C pools in one study (e.g. Fredeen *et al.*, 2005; Howard *et al.*, 2004; Hunt *et al.*, 2010; Martin *et al.*, 2005; Taylor *et al.*, 2007). However, pools like fine and medium roots, dead roots and stumps have not been studied in the context of total ecosystem C, resulting only partial understanding of ecosystem C dynamics.

2.2. Live biomass carbon

Live biomass is made up of overstory and under-story trees, shrubs, and ground vegetation, including both aboveground and belowground components. Although all components contribute to total biomass, overstory trees dominate the pool (**IV**). Except in young forest, where ground vegetation and regeneration are dominant (**II**). Therefore, total live biomass C follows the typical S-shape stand growth dynamics.

After stand replacing disturbance, live biomass C accumulates slowly at first, gradually speeding up and reaching a maximum rate, after which C accumulation slows. This type of dynamics is common in a wide range of forest ecosystems (Wardle *et al.*, 2004) and has also been reported in boreal forest by many studies (e.g. Martin *et al.*, 2005; Yermakov and Rothstein, 2006) and was also confirmed by study **II**. The relatively steady state of live biomass C is then normally ended by a stand replacing disturbance that, typically, in boreal forests, occur between 75–100 years after previous disturbance (Bergeron, 1991; Senici *et al.*, 2010; Weir *et al.*, 2000). Due to high disturbance frequency, stands might not reach the maximum biomass state.

Disturbance type strongly influences biomass C dynamics. Stand replacing wildfire kills nearly all vegetation, and live biomass accumulation will start from nearly zero. By contrast, after clearcut, a certain amount of advanced regeneration can be present and some overstorey trees might be left (depending on management objectives), resulting in higher biomass compared to burnt stands (**II**). Harvested sites are often regenerated artificially. Therefore, with all other aspects equal, harvested sites will have higher biomass than burnt sites at the early stage of stand development. They may reach maturity and the biomass decline phase earlier.

2.3. Dead biomass carbon

Dead biomass is made up of dead organic matter of different sizes and stages of decay, including standing dead trees, fallen dead trees (often referred to as DWD (downed woody debris), pieces >10 cm), stumps, roots (coarse, medium, fine) of stumps and standing dead trees and fine woody debris (2–10 cm) (**III**). Very fine woody debris (<2 cm) is commonly accounted for in the forest floor pool.

The dead biomass pool reflects the balance between input from live biomass and decomposition. Commonly, dead biomass in boreal forest follows a 'U' or 'S' shape mass curve after stand replacing disturbance (Brais *et al.*, 2005; Clark *et al.*, 1998; Martin *et al.*, 2005; Pedlar *et al.*, 2002; Sturtevant *et al.*, 1997; **I**). Dead biomass dynamics is similar after fire and harvest, but there are significant differences in the amount of dead wood.

Although fire often kills trees, it only consumes a fraction of their biomass via combustion (Kashian *et al.*, 2006). Fire also consumes only a fraction of pre-disturbance dead wood (8% of DWD) and another 8% is converted to charcoal (Tinker and Knight, 2001). These processes result in high dead wood mass after fire. Dead wood starts decomposing with low inputs in young stand, resulting in a decline in dead wood mass. Decrease continues until significant amounts of dead wood is being created by self-thinning. Thereafter, dead wood C mass starts to increase resulting in a 'U' shape curve (see paper **I**). The 'S' shape curve occurs when stands reach higher age and decomposition exceeds inputs.

With clearcut harvest, a considerable amount of live biomass is removed. This results in a much lower initial dead wood mass (**IV**). After, the

dynamics are similar to burnt stands. However, if stands have advance regeneration or are planted or seeded, the increase phase will start sooner than in burnt stands.

2.4. Forest floor carbon

The forest floor (FF) is the organic portion of the upper soil comprising of the LFH (Litter - Fermenting - Humified) horizons. The FF is made up of leaf litter, fine woody litter, and roots, and substantial amount of mineral soil can be mixed in from below by animals or other agents (Yanai *et al.*, 2003). Boreal forests build up substantial FF layers largely due to weather determined slow decomposition (Harden *et al.*, 1997). Depth of the FF in boreal mixedwoods can be up to 20 cm (Shrestha and Chen, 2010). The FF contains large amount of C and are nutrient rich and are a biologically active part of boreal forest soil (Krause, 1998). As it is the top layer of soil, it is more sensitive to temperature and moisture fluctuations and to disturbances than the mineral soil below (Khomik *et al.*, 2006). The FF contains *ca* 15% of C (Shrestha and Chen, 2010). Accumulation of C in the FF is primarily determined by stand species composition, productivity and regional climate (Nalder and Wein, 1999). Fire and harvesting influence FF C dynamics differently (Neff *et al.*, 2005; Shrestha and Chen, 2010; **IV**).

Stand replacing fire typically consumes most of the FF (Certini, 2005). With stand development, FF starts to accumulate and increase through stand development, reaching maximum in conjunction with maximum biomass state (Nalder and Wein, 1999; Pregitzer and Euskirchen, 2004; Rapalee *et al.*, 1998; Shrestha and Chen, 2010). By contrast, clearcut increases FF mass by created debris. After initial increase, FF mass starts to decrease due to an increased decomposition rate as a result of new stand conditions and lack of input. After reaching minimum, FF mass starts to increase and reaches maximum later than in burnt stands. The relatively stable state continues until disturbance.

2.5. Mineral soil organic carbon

Due to its vast amount in forest ecosystems, mineral soil C plays an important part in C dynamics. Organic C in mineral soil is commonly assessed within 1 m depth (Chen and Shrestha, 2012). Amount of soil

organic C (SOC) is determined by balance between C inputs from litterfall and rhizodeposition and C release through decomposition (Jandl *et al.*, 2007). Fine roots are the main source of SOC as they turnover more easily to soil than aboveground litter (Ruess *et al.*, 1996). SOC dynamics in boreal forest soils can be explained by the difference between fine root productivity and turnover (Steele *et al.*, 1997).

Forest fires can affect soil physical, chemical, mineralogical, and biological properties and the effects are dependent on fire duration and peak temperatures (Certini, 2005). Although fires influence mineral soil in various ways, it has been difficult to quantify changes in soil C and describe dominant dynamics as mineral soil C pool is highly variable (Pregitzer and Euskirchen, 2004). Overall, an increasing trend with time can be observed (Pregitzer and Euskirchen, 2004).

More detailed literature review of boreal forest C dynamics can be found in paper **I**.

3. AIMS OF THE STUDY

This thesis looks closely at boreal mixedwood forest C pools and their dynamics during stand development. Primary aim is to study total ecosystem C and all the components it is comprised of so that thorough overview can be given. To find out how anthropogenic disturbances influence forest ecosystems compared to natural disturbances, two main boreal disturbances are studied.

The specific aims of this doctoral thesis were to:

1. Quantify in detail boreal forest ecosystem C dynamics of main C pools:
    a. Live biomass C;
    b. Dead biomass C;
    c. Forest floor C;
    d. Mineral soil organic C.

2. Describe forest ecosystem C dynamics in natural forest;

3. Compare C dynamics of two prominent disturbances; wildfire and clearcut harvest.

It is hypothesised that as biomass is removed from harvested stands but largely remains in burnt stands, burnt stands will contain larger total C stock compared to harvested sites in young forests.

4. MATERIAL AND METHODS

4.1. Study area

For all studies, the same study area was used. The studies were conducted in the boreal mixedwood forest located ca 150 km north of Thunder Bay and ca 100 km west of Armstrong, Ontario, Canada between 49°27' N to 49°38' N and 89°29' W to 89°54' W with 350–370 m in elevation. The study area belongs to the Lake Nipigon ecoregion and Moist Mid-Boreal ecoclimatic region (Ecological Stratification Working Group, 1996). This ecoregion surrounds Lake Nipigon and extends westward from the north shore of Lake Superior to Lake St. Joseph in north western Ontario and is characterized by warm summers and cold, snowy winters. Mean annual temperature of –1.2 °C and mean annual precipitation of 725 mm (503 mm of rainfall and 253 mm of snow) recorded at Armstrong (50°17' N, 88°54' W, 320 m elevation), Ontario, the closest meteorological station to study area (Environment Canada, 2008). The growing season is approximately 160 days long with a mean growing season temperature of 12.3 °C (Environment Canada, 2008). Topographic features in this area were shaped by the retreat of the Laurentide Ice Sheet approximately ten millennia ago.

The vegetation of the study area is dominated in the overstory by trembling aspen (*Populus tremuloides* Michx.), jack pine (*Pinus banksiana* Lamb.), black spruce (*Picea mariana* [Mill.] B.S.P), paper birch (*Betula papyrifera* Marsh.). White spruce (*Picea glauca* [Moench] Voss) and balsam fir (*Abies balsamea* [L.] Mill.) are also present as minor components (Brassard *et al*., 2008; **II**). Understory plant species common in the area are mountain maple (*Acer spicatum* Lam.), dwarf raspberry (*Rubus pubescens* Raf.), alder (*Alnus* spp.), beaked hazel (*Corylus cornuta* Marsh.), bush honeysuckles (*Diervilla lonicera* Mill.), bluejoint reedgrass (*Calamagrostis canadensis* Michx.), blue-bead lily (*Clintonia borealis* Raf.), Canadian mayflower (*Maianthemum canadense* Desf.), three-leaf goldthread (*Coptis trifolia* Salisb.), violet (*Viola* spp.) and large-leaved aster (*Aster macrophyllus* L.). Detailed information on understory vegetation abundance, diversity and composition can be found in Hart and Chen (2008).

Soils are relatively deep glacial tills of the Brunisolic and Podzolic orders (Shrestha and Chen, 2010; Soil Classification Working Group, 1996).

Wildfire is the main natural and clearcut harvest the main anthropogenic disturbances, with an average fire return interval of approximately 100 years for the past century (Senici *et al.*, 2010).

4.2. Study design

This study uses space for time substitution (i.e., chronosequence) method for studying long term forest dynamics (Walker *et al.*, 2010). In 2007, two chronosequences were established, one after wildfire, one after harvest. Time since disturbance (TSD) is used instead of 'age' because the age of trees in older stands is much younger than the time since last disturbance, as the trees regenerated gradually as the second cohort under pioneer species.

To represent the development of a common boreal mixedwood successional pathway (Taylor and Chen, 2011) after stand replacing wildfire, stands were chosen to represent all developmental phases; stand initiation (1- and 8-year-old stands), stem exclusion (27-year-old stands), canopy transition (85- and 140-year-old stands), and gap dynamics (203-year-old stands) (Chen and Popadiouk, 2002). Ages of chosen stands were determined by the fire history of the area (Hart and Chen, 2008). All sites regenerated naturally without any subsequent anthropogenic disturbance.

Since large scale commercial logging began in the area in the early 1970s, post clearcut stands represent only early stages of forest development (e.g. stand initiation and stem exclusion phase). All post logged stands were clearcut-harvested, but differed somewhat in the logging method. In the 1- and 9-year-old stands, trees were felled and dragged to roadside for processing. In 27-year-old stands, trees were felled, topped, and delimbed at the stump before being dragged to roadside. After logging, all cut sites were artificially regenerated (aerial seeding with *Pinus banksiana*) to achieve desirable species composition and fast regrowth. Each stand age class and origin was replicated three times, resulting in 27 sampled stands.

At any stage of development, stands in the study area can be dominated by conifer, deciduous or mixture of these species (Taylor and Chen, 2011). This thesis is focused on the most common successional pathway i.e., Dominance of *Populus tremuloides* and *Pinus banksiana* at the early stages and *Picea* spp., *Abies balsamea* and *Betula papyrifera* at the late stages of stand development (Taylor and Chen, 2011).

To reduce the effect of site conditions on C dynamics, all sites were selected on flat, mid-slope positions, with no slope exceeding 5%, on well-drained glacial moraines >50 cm in thickness, which is the prevailing site type in the region. To ensure each selected site met the criteria, a soil pit was dug in each sampled stand to verify whether the site was mesic following the procedure described in Taylor *et al.* (2000). All selected stands were at least one ha in area and were visually homogeneous in structure and composition.

TSD was known from records for younger stands (i.e. 1, 8 and 27). To determine the age of older stands for study **II**, first, fire records were consulted (Senici *et al.*, 2010) and then, the age was verified in the field by increment cores (Hart and Chen, 2008).

Paper **I** is a literature review. For paper **II** all 27 sites were used. For paper **III** the vicinity of the chronosequence sites was used. For paper **IV** only the first three age classes after fire and harvest were used.

Measured components:

- Live biomass:
    1. All size trees and shrubs (MS);
    2. Understory vegetation (vascular plants, lichens) (MS);
    3. Coarse roots (>10 mm) (BB);
    4. Medium roots (2–10 mm) (ZY);
    5. Fine roots (<2 mm) (ZY).
- Dead biomass:
    1. Standing dead trees (MS);
    2. Stumps (MS);
    3. Downed woody debris (MS);
    4. Dead coarse roots (BB, MS);
    5. Dead medium and fine roots (ZY).
- Forest floor (BS)
- Mineral soil organic C:
    1. 0–15 cm horizon (BS);
    2. 16–30 cm horizon (BS);
    3. 31–100 cm horizon (JL) (average for all sites).

Data was collected by: BB – Brian Brassard, BS – Bharat Shrestha, JL – Jérôme Laganière, MS – Meelis Seedre, ZY – Zhiyou Yuan.

4.3. Data collection

In selected sample stands a 400 m^2 circular plot was established. Live vegetation was measured within the plots. Tree biomass was calculated from DBH and height using allometric equations (Lambert *et al.*, 2005). Understory vascular plant biomass was harvested for measurements. Individual coarse root (>10 mm in diameter) biomass estimates were calculated using published allometric root biomass equations based on DBH (Bond-Lamberty *et al.*, 2002; Brassard *et al.*, 2011). Medium (2–10 mm diameter) and fine (<2 mm diameter) root biomass data was collected from each 400 m^2 circular plot and was determined by soil coring every month from May to September, average mass of these months is used.

Snags and stumps were measures inside the 400 m^2 circular plot. Snags included both dead trees with and without branches. Mass of snags with top was calculated using live tree allometric equations and results were adjusted for decay. Mass of snags with broken top and stumps (height <1.3 m) was calculated using truncated cone formula. The biomass of

dead coarse roots of snags and stumps was calculated similar to live coarse roots and adjusted for decay. Biomass of dead medium and fine roots was determined like live medium and fine root biomass. Downed woody debris mass was estimated using two 50 m transects radiating from the circular sample plot center. The DWD volume was calculated according to Husch *et al.* (2003). Volume of different components was converted to biomass using site specific dead biomass density values developed for study **III**.

Forest floor and mineral soil samples were collected within a 0.1 ha area surrounding the main 400 m^2 circular plot from six random points. Samples of FF layer and top mineral soil (0–15 and 15–30 cm) were collected from all sites. Deeper soil samples (30–100 cm) were collected from different sites from the study area (Laganière *et al.*, 2013) and used as no significant change is expected in deeper soil following disturbance (Goulden *et al.*, 2011; Harden *et al.*, 1997; Wirth *et al.*, 2002). Bulk density of FF was determined by weighing three 10 ml replicates of air dried, sieved samples (Shrestha and Chen, 2010). Mineral soil bulk density was determined by drying samples in an oven at 105 ºC until a constant weight (48 hours), and corrected for stone volume. Soil samples were tested for C content using dry combustion method (McGill and Figueiredo, 1993) using LECO CNS 2000.

Carbon content was assumed to be 50% of oven dry wood tissue and 45% of foliage tissue (Bisbee *et al.*, 2001; IPCC, 2003). The carbon content of DWD, snags and stumps was assumed to be 50% of dry biomass (Garrett *et al.*, 2012). Carbon content of vascular plants, bryophytes, medium and fine roots was assumed to be 45% of dry biomass (Bisbee *et al.*, 2001; IPCC, 2003). All pools were scaled-up to Mg C ha^{-1}.

Detailed description of methods can be seen in each respective paper.

4.4. Data analysis

Mean stand-level estimates (Mg C ha^{-1}) for each carbon pool, in each age-class, were calculated (Table 1). Data was first tested for normality with *A Shapiro-Wilk* test and for homogeneity of variance with *Levene's* Test. If necessary, data transformations were performed (square root and natural logarithm). Linear models were used to test if C pools change

with time since disturbance and/or are different between disturbances. Post hoc tests were used after to determine which means (or densities for paper **III**) differ significantly. Total ecosystem C was calculated for each replicate stand and age class by summing all individual ecosystem C pools (Table 1). SPSS 11 (SPSS, 2001) and R (R Core Team, 2012) were used for analysis.

5. RESULTS

Total ecosystem C (TEC) changed significantly with TSD ($P<0.05$) but there were no differences between disturbance types (Table 2; Figure 1). After harvest, total ecosystem C declined from 146.5 to 127.7 Mg C ha^{-1}, then increased to 185.1 Mg C ha^{-1} by year 27 (Figure 1e). After fire, total ecosystem C also declined, from 133.7 Mg C ha^{-1} to 127.4 Mg C ha^{-1} and reached 163.6 Mg C ha^{-1} by year 27.

Over time, the contribution of each component to TEC varied (Figures 2a, 2b, 2c, 2d). Live biomass C, forest floor C, and mineral soil C changed differently after fire and harvest, while dead wood change was similar between disturbances. There was significantly more live biomass C one year after harvest, then C mass became similar, but at year 27 harvested forest live biomass C was higher again (Figure 2a). The initial difference was mostly due to differences in aboveground biomass C between burnt and harvested stands (Figure 3a). The higher biomass C in 27-year-old stands was due to aboveground biomass and coarse root biomass (Figures 3a and 3b). There was no difference between disturbances in fine and medium root C mass (Figure 3c). After fire, fine and medium root C mass increased significantly but remained the same after harvest (Figure 3c).

Total dead biomass C decreased similarly after fire and harvest (Figure 2b). There were significant differences between burnt and harvested forest dead wood C one year after disturbance, however, as stands developed the differences became insignificant (Figure 3b). This difference is mostly due to higher snag and stump C mass after fire (Figure 4a). A significant drop in the snag and stump C pool after year 1 corresponds to increases in the DWD pool at year 8 (Figures 4b and 4c). Dead medium and fine root C decreased after disturbances and differed between disturbance types (Figure 4c).

Forest floor and mineral soil C mass was not different between disturbances (Table 2; Figures 2c and 2d). There was no significant change in forest floor and mineral soil C after harvest, but both pools increased significantly after fire (Figures 2c and 2d).

Table 1. C stocks of different forest ecosystem components (Mg C ha^{-1}). (Continues on next page) (IV).

	Age class											
	1				8				27			
Carbon Pool	cut		fire		cut		fire		cut		fire	
Live Aboveground Vegetation												
Large trees (>10 cm DBH)	8.4	2.1	0.0	0.0	0.0	0.0	0.0	0.0	48.0	3.0	1.0	0.3
Small trees (<10 cm DBH)	0.0	0.0	0.0	0.0	2.4	0.0	3.1	1.3	3.7	1.7	12.2	1.6
Herbs and Shrubs	0.0	0.0	0.1	0.0	0.2	0.0	0.3	0.1	0.3	0.1	0.1	0.1
Bryophytes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.1	0.3	0.1
Live Belowground Vegetation												
Coarse roots (≥10 mm)	2.3	0.5	0.0	0.0	0.7	0.1	0.7	0.2	15.7	0.9	2.4	0.3
Medium and fine roots (<10 mm)	4.5	0.9	2.8	0.5	4.4	2.6	5.1	0.5	7.2	1.9	7.5	1.0
Total Live Vegetation	**15.3**	**2.9**	**3.0**	**0.3**	**7.7**	**1.7**	**9.2**	**1.4**	**75.1**	**4.5**	**23.5**	**1.7**

* Numbers after stocks are ±1 SE (n = 3).

Table 1. (continued). C stocks of different forest ecosystem components (Mg C ha^{-1}) (IV).

	Age class											
	1				8				27			
Carbon Pool	cut		fire		cut		fire		cut		fire	
Dead Vegetation												
Aboveground snags and stumps	1.2	0.2	47.9	4.3	5.3	0.8	7.7	2.7	4.1	1.3	1.0	0.3
Belowground snags and stumps	21.7	2.5	18.3	1.8	20.6	3.6	8.8	0.5	6.8	3.2	2.4	0.9
Medium and fine roots (<10 mm)	2.4	0.4	1.4	0.3	1.5	0.4	0.8	0.3	0.6	0.0	0.7	0.1
Downed woody debris	14.8	0.4	9.6	1.0	8.0	1.4	30.3	5.6	1.6	0.7	21.5	4.3
Total Dead Vegetation	**40.2**	**2.2**	**77.2**	**6.1**	**35.4**	**5.8**	**47.6**	**2.9**	**13.2**	**4.9**	**25.7**	**3.1**
Forest floor	**29.2**	**2.7**	**3.4**	**0.9**	**27.7**	**9.2**	**26.9**	**8.6**	**41.4**	**6.9**	**50.2**	**8.7**
Mineral Soil (0–100 cm)												
Top layer (0–30 cm)	38.7	3.0	27.0	1.3	33.6	4.9	20.5	1.3	32.3	4.7	41.1	5.5
Lower layer (31–100 cm)	23.2		23.2		23.2		23.2		23.2		23.2	
Total Mineral Soil	**61.8**	**3.0**	**50.2**	**1.3**	**56.8**	**4.9**	**43.7**	**1.3**	**55.5**	**4.7**	**64.3**	**5.5**
Total Ecosystem Carbon	**146.5**	**7.4**	**133.7**	**5.8**	**127.7**	**19.5**	**127.4**	**8.5**	**185.1**	**18.4**	**163.6**	**7.9**

* Numbers after stocks are ±1 SE (n = 3).

Table 2. Time since disturbance (TSD), disturbance type (D) and their interaction effects on ecosystem C pools (IV).

	TSD (df=2)		D (df = 1)		TSD x D (df = 2)	
C Pool	F	*P*	F	*P*	F	*P*
Live biomass C						
Aboveground biomass *	8.9	**<0.001**	2.3	**<0.001**	1.5	**<0.001**
Coarse roots *	2.8	**<0.001**	1.2	**<0.001**	0.9	**<0.001**
Medium roots	20.4	**0.002**	0.4	0.543	5.9	**0.072**
Fine roots *	0.2	**0.003**	0.0	0.766	0.0	0.774
Total roots *	2.4	**<0.001**	0.5	**0.001**	0.5	**0.003**
Total biomass *	7.5	**<0.001**	1.9	**<0.001**	1.4	**<0.001**
Dead biomass C						
Aboveground snags and stumps*	2.6	**<0.001**	2.1	**<0.001**	6.2	**<0.001**
DWD	212.4	**0.047**	678.3	**<0.001**	691.3	**<0.001**
Dead coarse roots	732.8	**<0.001**	192.7	**0.006**	62.8	0.200
Dead medium and fine roots	5.0	**0.002**	1.3	**0.035**	1.0	0.159
Total dead roots	852.1	**<0.001**	225.4	**0.004**	67.0	0.200
Total dead wood	4646.4	**<0.001**	1902.0	**<0.001**	613.1	**0.023**
Forest floor and mineral soil C						
Forest floor	2667.7	**0.004**	157.2	0.318	959.2	**0.072**
Mineral soil 0–100 cm	283.2	**0.076**	126.9	0.116	449.6	**0.025**
Total ecosystem C						
Total ecosystem	7044.1	**0.008**	599.7	0.281	345.9	0.700

transformed data. Note: Significant ($p<0.05$*) and marginally significant (*$p = 0.06 – 0.1$*) values are in bold.*

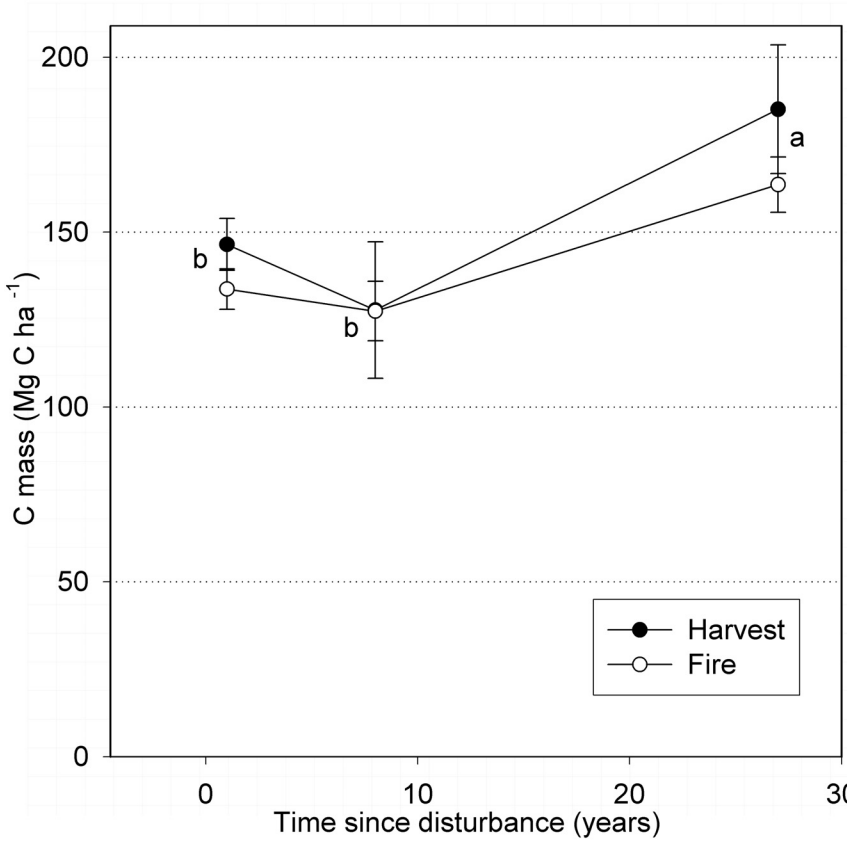

Figure 1. Total ecosystem C pool after harvest and fire in relation to time since disturbance. Symbols represent stand means for each age class (±1 SE; n = 3). Note: Different letters indicate significant difference based only on effects of TSD (**IV)**.

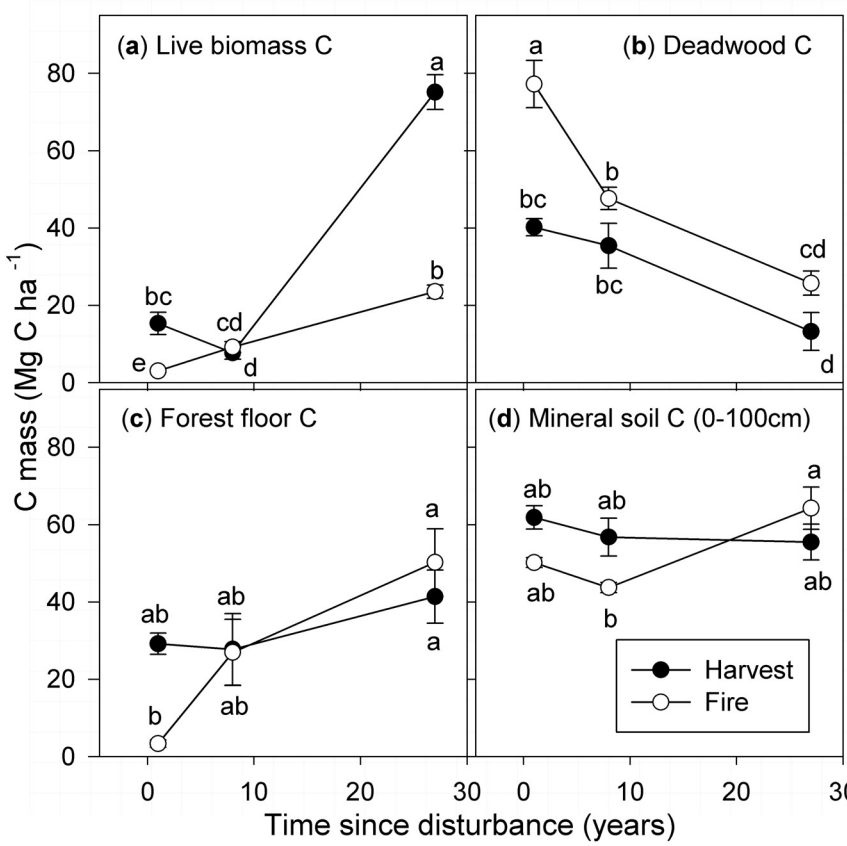

Figure 2. Main C pools after harvest and fire in relation to time since disturbance for: a) Live biomass; b) Dead biomass; c) Forest floor and d) Mineral soil (0–100 cm). Symbols represent stand means for each age class (±1 SE; n = 3). Note: Different letters indicate significant difference (**IV)**.

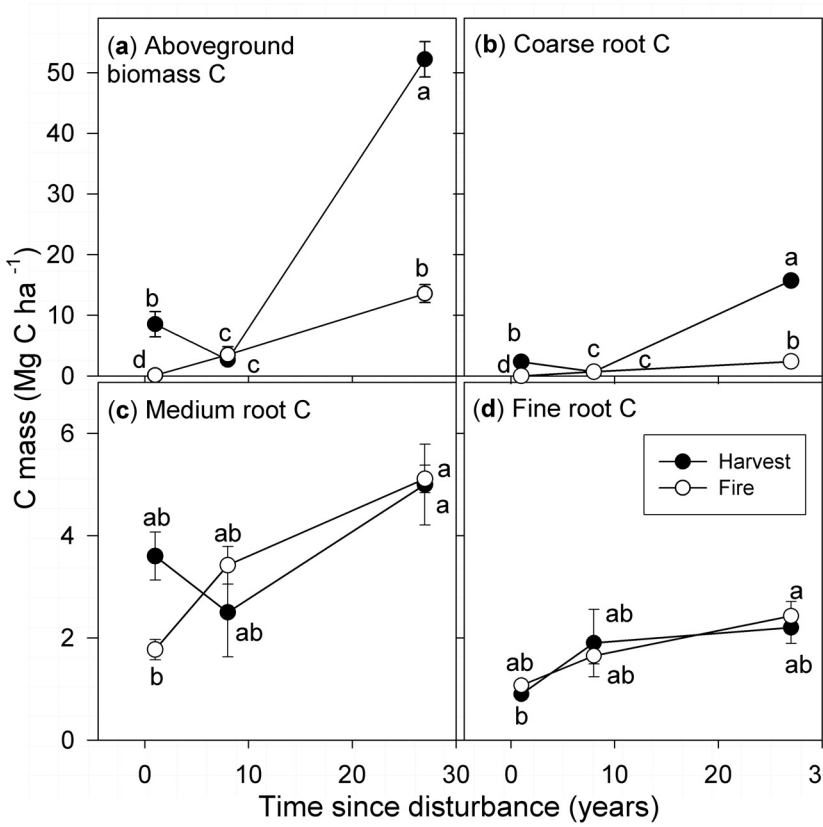

Figure 3. Live biomass C pools after harvest and fire in relation to time since disturbance for: a) Aboveground biomass; b) Coarse roots; c) Medium roots and d) Fine roots. Symbols represent stand means for each age class (±1 SE; n = 3). Note: Different letters indicate significant difference. Y axes are different (**IV)**.

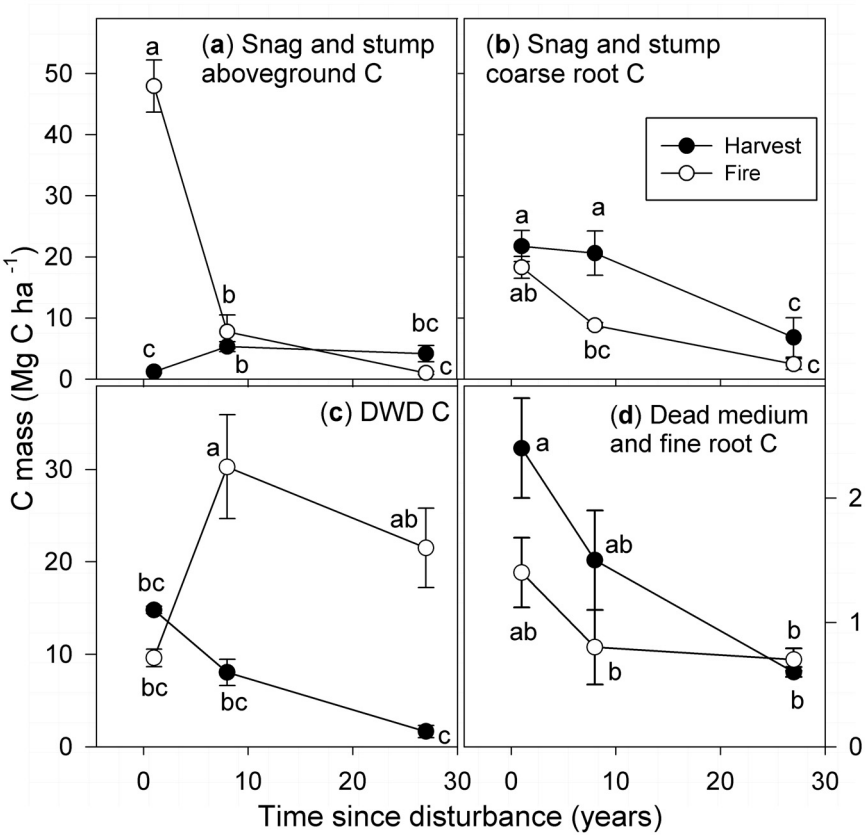

Figure 4. Dead biomass C pools after harvest and fire in relation to time since disturbance for: a) Snag and stump aboveground; b) Snag and stump coarse roots c) Down woody debris (DWD) and d) Dead medium and fine roots. Symbols represent stand means for each age class (±1 SE; n = 3). Note: different letters indicate significant difference. Y axes are different (**IV)**.

All pools contributed considerably to total ecosystem C, dead wood and mineral soil C being the most prominent (Figures 2b and 2d; Figure 5a). Live biomass C, in general, made up 14% of total ecosystem C, 19% in harvested and 8% in burnt sites (Figure 5a). Only in 27-years-old harvest sites was the live biomass share higher (41%). Dead wood made up 7–58% of total C, averaging at 21% in harvested sites and 37% in burnt sites. Forest floor ranged from 3–31%, averaging 20%. Mineral soil C percentage was high similar to dead wood, averaging 38% of total ecosystem C. From total ecosystem C, all aboveground C (including forest floor) made up 58% in harvested sites and 49% in burnt sites.

Aboveground live biomass made up less than half of total live biomass (43%) (Figure 5b), 53% in harvested and 33% in burnt sites. From total live biomass, medium and fine roots (21% in harvested and 41% in burnt sites) were more abundant than coarse roots (15% in harvested and 6% in burnt sites) and fine roots (11% in harvested and 16% in burnt sites).

The downed woody debris and belowground dead wood were the prominent dead wood C pools, both representing 39% of total dead wood (Figure 5c). However, share of these pools was different after harvest and fire. DWD made up 24% in harvested and 53% in burnt sites, belowground dead wood 59% in harvested and 20% in burnt sites. Stumps constituted 11% in harvested sites and 3% in burnt. Snags 6% in harvested and 25% in burnt sites.

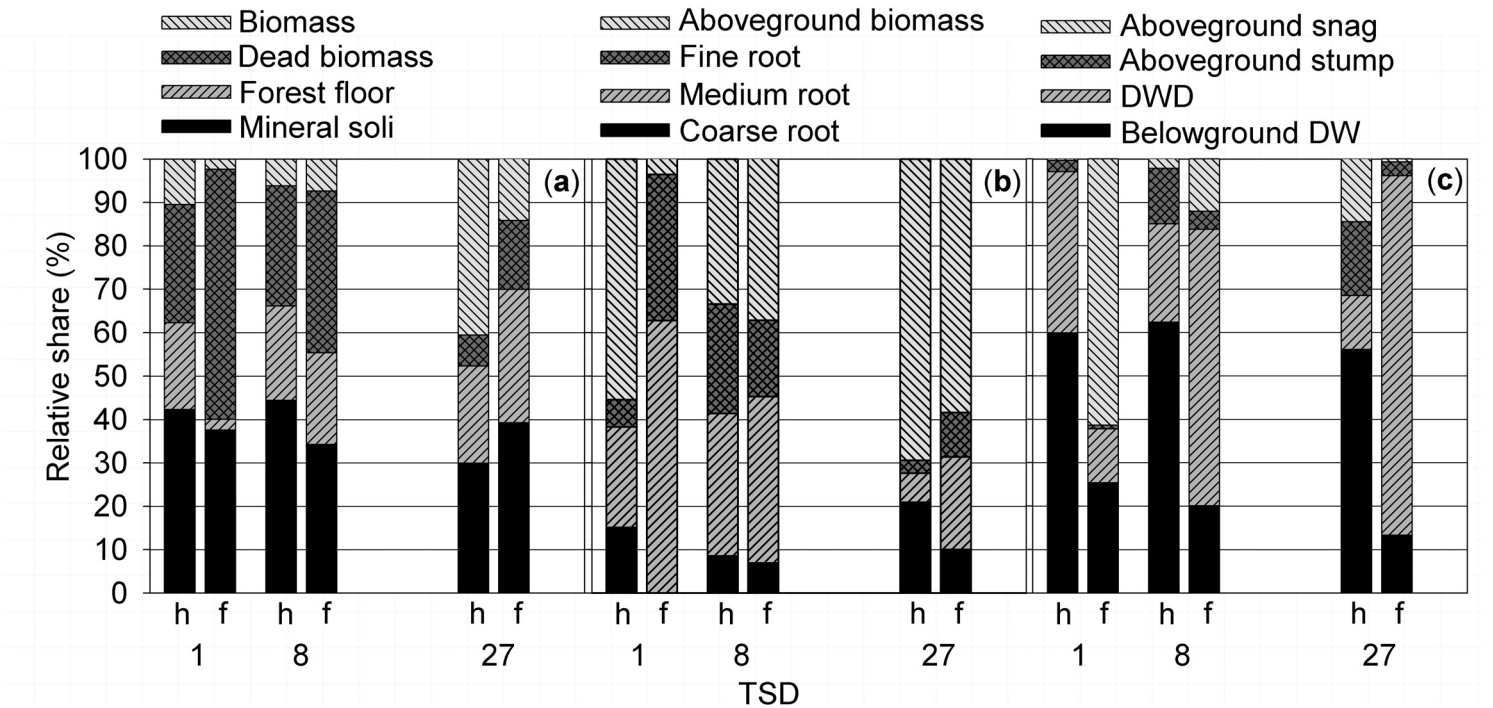

Figure 5. Relative share of forest ecosystem C pools for: a) total ecosystem; b) total live biomass and; c) total dead biomass. Note: h stands for harvest and f for fire (**IV**).

6. DISCUSSION

The detailed C database compiled for this study clearly shows that regardless of significant differences in individual C pools, total ecosystem C (TEC) does not differ between natural and managed young boreal forests. Therefore, primary hypothesis of the thesis has to be rejected. Higher C mass in harvested sites shortly after disturbance in live biomass, forest floor and mineral, but lower C mass in dead biomass, resulted in similar total C after both disturbances. Eight years after disturbance, live biomass and forest floor C were also similar after both disturbances. Higher dead biomass in burnt sites and lower mineral soil C in harvested sites resulted in nearly identical TEC. At year 27, higher live biomass C in harvested sites and lower C mass in other pools compared to burnt stands resulted in similar TEC.

Therefore, current management practices (i.e. harvesting and planting or seeding) in boreal mixedwood forests of central Canada have no negative impact on TEC. Considering also the life cycle of products made from this wood and the displacement effect (i.e. use of wood instead of concrete or steel that have higher C footprint) (Gower, 2003; Micales and Skog, 1997; Sathre and O'Connor, 2010), shows that harvesting results an increased C uptake from the atmosphere, therefore moderating climate change. However, harvesting can result in lower TEC when live biomass growth is slow (failed or insufficient regeneration) and the C content in mineral soil does not increase. The lower dead wood level in harvested sites would result in lower TEC in harvested forests. Consequently, success of silvicultural techniques to achieve rapid tree growth are vital in C capture and high TEC that is at least as high as in natural forests and with good management practices to help lower atmospheric C concentration compared to natural stands.

6.1. Total ecosystem carbon

The dynamics of different C pools followed dynamics commonly observed in boreal forests (**I**) and our results are in general agreement with other studies reporting TEC, with some differences likely due to forest type and local conditions. A study in mixedwood boreal stands of Manitoba found similar TEC levels in harvested stands (Martin *et al.*, 2005). In 11-year-old stands, they report 126.9 Mg C ha^{-1} TEC and in this study

there is 104.6 Mg C ha^{-1} TEC at year 8 (including only 0–30 cm mineral soil C, similar to Martin *et al.*, 2005 study). In 30-year-old stands, they report 114.7 Mg C ha^{-1} TEC. In this study, at year 27, the amount is much higher (161.9 Mg C ha^{-1}), mainly due to higher vegetation C (also including only 0–30 cm mineral soil C). TEC in harvested jack pine stands in Saskatchewan was less than half of what was found in this study (Howard *et al.*, 2004). This is in part because they only measured mineral soil C up to 20.4 cm depth. However, their pure jack pine stands had also considerably less live biomass, dead biomass and forest floor C than mixedwood stands. Black spruce stands of eastern boreal forest (Newfoundland) have higher TEC than our boreal mixedwood sites (Moroni *et al.*, 2010). Young (0–2 years) harvested sites had 164.8 Mg C ha^{-1} and burnt (2–3 years) sites 157.8 Mg C ha^{-1}, while our sites had 146.2 and 133.8 Mg C ha^{-1} after harvest and fire, respectively. Harvested black spruce forests of 31–36 years had 216.2 and burnt 31-years-old sites 202.9 Mg C ha^{-1} while our 27-year-old sites had 185.1 and 163.6 Mg C ha^{-1} after harvest and fire, respectively. These differences are mainly due to considerably higher forest floor and mineral soil C in Newfoundland boreal forests, even though they report 0–45 cm depth mineral soil C. Mixedwood TEC levels are also similar to temperate softwood forest stands of Nova Scotia (Taylor *et al.*, 2007).

6.2. Live biomass carbon

Total (above and belowground) live biomass C dynamics largely followed aboveground biomass C dynamics (**II**). After harvest, live biomass C was significantly higher than after fire due to some large overstory trees left standing (ecological considerations) during harvest, while in our sites no large trees survived fire (**II**). Also, fire killed nearly all small trees, but many small trees survived harvest and became advanced regeneration. Much higher live biomass in 27-year-old post-harvest stands can be mostly attributed to successful seeding that aided in faster stand establishment than in burnt stands. Burnt stands will likely achieve biomass levels as high as managed stands later stages of stand development. Therefore, same area of forest can capture more C in live biomass earlier when managed successfully compared to natural stands. Management of forest stands should be preferred when maximizing C capture is desired. However, it is necessary to make detailed comparisons also in older forests. Harvesting began only recently in the area and long term comparisons were not possible for this study.

6.3. Dead biomass carbon

Dead biomass C decreased similarly after fire and harvest, but there was significantly more total dead biomass C right after fire. However, later in stand development the differences in total dead biomass C became non-significant. Higher dead biomass C in fire sites resulted from very high aboveground snag and stump C. This was expected as even stand replacing high intensity wildfire only consumes a fraction of biomass (Kashian *et al.*, 2006). There were no differences in other dead biomass pools right after disturbance. Most snags fell a few years after disturbance and in 8-year-old burnt stands the DWD C mass was significantly higher compared to harvested sites. After fire, C moved from snag and stump pool to the DWD and thereafter to FF pool. It has been found that fire created dead vegetation decomposition can cause even greater C release than fire event (Kashian *et al.*, 2006). As much as three times more C can be released to atmosphere via dead wood decomposition following wildfire than during wildfire (AuClair and Carter, 1993). In our study burnt sites lost ca. 40 Mg C ha^{-1} of snag and stump C and gained ca. 20 Mg C ha^{-1} of the DWD C and ca. 25 Mg C ha^{-1} of the FF C. After year 8, total dead wood C decreased significantly in both burnt and harvested sites. This decrease can be attributed mainly to decomposition of the DWD and belowground dead wood C pool decrease.

6.4. Forest floor carbon

Differences in the FF mass after harvest and fire are inherent as lots of debris is created during harvest operations contrary to nearly complete consumption of the FF by stand replacing wildfire. Forest floor C mass did not change after harvest, but increased significantly after fire. Although harvesting created a lot of debris, increased decomposition due to new opened conditions might explain stable FF mass after harvest. After fire there is almost no FF left since stand replacing fire consumes much of the FF mass (Certini, 2005; Yanai *et al.*, 2003). However, soon after fire, recently died biomass starts to break down creating significant increase in the FF mass. Higher resistance of burnt wood to decay adds to the FF C increase in burnt sites (Shorohova *et al.*, 2012). The result is significantly increased (up to 50 Mg C ha^{-1} in year 27) FF C mass in burnt sites to levels similar to harvested sites.

6.5. Mineral soil organic carbon

Similarly to the FF, mineral soil C mass, did not change after harvest and increased significantly after fire. Accumulation of C in boreal forest mineral soil is mostly explained by fine root production and turnover (Steele *et al.*, 1997). Our data supports this hypothesis when also medium roots are considered. It takes some time for C to move from fine and medium root C pools to the mineral soil C pool. Therefore, we see no differences between burnt and harvested sites directly after disturbance. After some time, however, effects of changed fine and medium root production are reflected in mineral soil C pool by a small decrease in the C mass. Then, fine and medium root mass (reflecting production) increased in burnt sites and at the same time significant increase of mineral soil C took place. In harvested sites, fine and medium root mass did not change between 1- and 8-year-old sites but was higher in 27-year-old sites and no change in mineral soil pool took place. This increase in mineral soil C pool might take place after. Although other factors (e.g. incorporation of organic material from FF) also influence mineral soil C dynamics, fine and medium roots seem to play a prominent role. Contrary to meta-analysis of 13 studies looking at mineral soil C that found that fire has no effect on mineral soil C (Johnson and Curtis, 2001), our data indicates that boreal mixedwoods mineral soil C is affected by wildfire because it affects root turnover.

6.6. Carbon allocation

All C pools contributed substantially to the TEC. Mineral soil and dead wood dominated in the early stages (year 1 and 8) of stand development, making-up 71% and 83% of the TEC after harvest and fire, respectively. These results illustrate the importance of including all C pools when studying ecosystem C. Exclusion of any pool would have given significantly different results. An interesting result is that at the beginning of forest development, approximately half of the TEC is visible (aboveground live biomass and dead biomass).

The share of belowground dead wood C was much higher in harvested sites than burnt sites, ca 60% vs 20%, respectively. This is in-part due to higher DWD and snag C in burnt sites, but also, as total belowground dead wood mass was higher in harvested sites these results might also indicate

some drawbacks in belowground dead biomass sampling methodology. Burnt forest belowground dead wood C might be underrepresented as during high intensity fire stump dimensions were decreased due to burning (personal observation) and dead root mass calculated therefore smaller than actual dead root mass. These burnt stumps likely decayed slower than non-burnt stumps in harvested sites (Shorohova *et al.*, 2012), resulting smaller underrepresentation of dead coarse roots later in stand life. It would be useful to study how much stump diameters are decreased during stand replacing wildfire and compensate for that in mass calculations.

7. CONCLUSIONS

A comprehensive C database was compiled for this study including all major forest ecosystem C pools. Based on a chronosequence approach we found that in young Boreal forests the total ecosystem carbon mass does not differ between harvested and burnt forests. However, different C pools responded differently to disturbance events.

There was significantly more live biomass C right after harvest compared to burnt stands. This was because fire killed nearly all vegetation but after harvest some residual live trees were left on site and also unharmed advanced regeneration was present. Higher live biomass C in 27-year-old stand can be attributed to successful silvicultural techniques, as due to artificial regeneration trees started to grow earlier than in natural stands.

There was significantly more dead biomass in burnt stands right after disturbance compared to harvested stands. This is because during fire trees are killed but not much of them are actually burnt. Contrary, during harvest, lot of material is removed for human consumption resulting this inherent difference with burnt sites. The difference is well seen in snag and stump C pool. After initial difference, the dead biomass C pool became similar between disturbances but decreased significantly after fire and harvest. Part of this C was released through decomposition and another part allocated to forest floor C pool.

Forest floor C increased significantly after fire but remained stable after harvest. Forest fire consumes much of the forest floor but during harvest forest floor mass can be even increased due to disturbance created debris. Later in development forest floor mass becomes similar after both disturbances.

Mineral soil C did not differ significantly between disturbances. Also, there was no change of this pool after harvest but a significant increase after fire from 8-year-old sites to 27-year-old sites. This increase is possibly explained by increased medium and fine root production that did not take place after harvest.

Unlike many other studies that do not consider all C pools, we were able to collect data from most relevant pools. Pools that are commonly not studied in works reporting total ecosystem are fine and medium

roots, coarse roots, stumps, and we have not found a study where dead roots were included. Methodology to estimate dead coarse root mass was developed for this study. We found that all pools contribute considerably to total pool. Due to the inclusion of nearly all major ecosystem C pools we can be reasonably certain of our results about total ecosystem carbon.

There is no difference between natural and anthropogenic disturbance on total ecosystem C in young forest. Therefore, use of harvesting products decreases atmosphere CO_2 content and moderates climate change. In the end of harvested product life cycle much of captured carbon is released back to atmosphere but not all. It is also important to consider raw material replacement effect (use of wood instead of concrete or metal). To decrease atmospheric CO_2 concentration it is better to use a renewable low carbon footprint material like wood instead of other materials. Therefore good forest management that results high productivity is a practice that decreases human influence on climate. It is necessary in future to compare total ecosystem C also in older forests after natural and anthropogenic disturbances to estimate management effect on C later in stand development.

REFERENCES

AuClair, A.N.D., Carter, T.B. (1993) Forest Wildfires As A Recent Source of Co2 at Northern Latitudes. Canadian Journal of Forest Research 23, 1528–1536.

Banfield, G.E., Bhatti, J.S., Jiang, H., Apps, M.J. (2002) Variability in regional scale estimates of carbon stocks in boreal forest ecosystems: results from West-Central Alberta. Forest Ecology and Management 169, 15–27.

Bergeron, Y. (1991) The Influence of Island and Mainland Lakeshore Landscapes on Boreal Forest-Fire Regimes. Ecology 72, 1980–1992.

Bisbee, K.E., Gower, S.T., Norman, J.M., Nordheim, E.V. (2001) Environmental controls on ground cover species composition and productivity in a boreal black spruce forest. Oecologia 129, 261–270.

Bonan, G.B. and Shugart, H.H. (1989) Environmental factors and ecological processes in boreal forests. Annual review of ecology and systematics 20, 1–28.

Bonan, G.B. (2008) Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. Science 320, 1444–1449.

Bond-Lamberty, B., Wang, C., Gower, S.T. (2002) Aboveground and belowground biomass and sapwood area allometric equations for six boreal tree species of northern Manitoba. Canadian Journal of Forest Research 32, 1441–1450.

Boulanger, Y., Sirois, L. (2006) Postfire dynamics of black spruce coarse woody debris in northern boreal forest of Quebec. Canadian Journal of Forest Research 36, 1770–1780.

Brais, S., Sadi, R., Bergeron, Y., Grenier, Y. (2005) Coarse woody debris dynamics in a post-fire jack pine chronosequence and its relation with site productivity. Forest Ecology and Management 220, 216–226.

Brassard, B.W., Chen, H.Y.H. (2006) Stand structural dynamics of North American boreal forests. Critical Reviews in Plant Sciences 25, 115–137.

Brassard, B.W., Chen, H.Y.H. (2008) Effects of Forest Type and Disturbance on Diversity of Coarse Woody Debris in Boreal Forest. Ecosystems 11, 1078–1090.

Brassard, B.W., Chen, H.Y.H., Bergeron, Y., Pare, D. (2011) Coarse root biomass allometric equations for *Abies balsamea*, *Picea mariana*, *Pinus banksiana*, and *Populus tremuloides* in the boreal forest of Ontario, Canada. Biomass & Bioenergy 35, 4189–4196.

Brassard, B.W., Chen, H.Y.H., Wang, J.R., Duinker, P.N. (2008) Effects of time since stand-replacing fire and overstory composition on live-tree structural diversity in the boreal forest of central Canada. Canadian Journal of Forest Research 38, 52–62.

Certini, G. (2005) Effects of fire on properties of forest soils: a review. Oecologia 143, 1–10.

Chen, H.Y.H., Popadiouk, R.V. (2002) Dynamics of North American boreal mixedwoods. Environmental Reviews 10, 137–166.

Chen, H.Y.H., Shrestha, B.M. (2012) Stand age, fire and clearcutting affect soil organic carbon and aggregation of mineral soils in boreal forests. Soil Biology & Biochemistry 50, 149–157.

Clark, D.F., Kneeshaw, D.D., Burton, P.J., Antos, J.A. (1998) Coarse woody debris in sub-boreal spruce forests of west-central British Columbia. Canadian Journal of Forest Research 28, 284–290.

Ecological Stratification Working Group, (1996) A national ecological framework for Canada. Agriculture and Agri-Food Canada, Research Branch, Centre for Land and Biological Resources Research, and Environment Canada, State of the Environment Directorate, Ecozone Analysis Branch, Ottawa, Ont.

Environment Canada (2008) Climate normals for Thunder Bay, ON, Canada (1971–2000) [online]. Environment Canada, Meteorological Service of Canada, Downsview, Ont. Available from http://www.climate.weatheroffice.ec.gc.ca/index.html [accessed on 23 December 2008].

Fleming, R. A., Volney, W. J. A. (1995) Effects of climate change on insect defoliator population processes in Canada's boreal forest: some plausible scenarios, Water, Air, and Soil Pollution 82, 445–454.

Fredeen, A.L., Bois, C.H., Janzen, D.T., Sanborn, P.T. (2005) Comparison of coniferous forest carbon stocks between old-growth and young second-growth forests on two soil types in central British Columbia, Canada. Canadian Journal of Forest Research 35, 1411–1421.

Garrett, L.G., Kimberley, M.O., Oliver, G.R., Pearce, S.H., Beets, P.N. (2012) Decomposition of coarse woody roots and branches in managed *Pinus radiata* plantations in New Zealand: a time series approach. Forest Ecology and Management 269, 116–123.

Goetz, S.J., Bond-Lamberty, B., Law, B.E., Hicke, J.A., Huang, C., Houghton, R.A., McNulty, S., O'Halloran, T., Harmon, M., Meddens, A.J.H., Pfeifer, E.M., Mildrexler, D., Kasischke, E.S. (2012) Observations and assessment of forest carbon dynamics following disturbance in North America. Journal of Geophysical Research-Biogeosciences 117.

Goodale, C.L., Apps, M.J., Birdsey, R.A., Field, C.B., Heath, L.S., Houghton, R.A., Jenkins, J.C., Kohlmaier, G.H., Kurz, W., Liu, S.R., Nabuurs, G.J., Nilsson, S., Shvidenko, A.Z. (2002) Forest carbon sinks in the Northern Hemisphere. Ecological Applications 12, 891–899.

Goulden, M.L., McMillan, A.M.S., Winston, G.C., Rocha, A.V., Manies, K.L., Harden, J.W., Bond-Lamberty, B.P. (2011) Patterns of NPP, GPP, respiration, and NEP during boreal forest succession. Global Change Biology 17, 855–871.

Gower, S.T. (2003) Patterns and mechanisms of the forest carbon cycle. Annual Review of Environment and Resources 28, 169–204.

Gower, S.T., Vogel, J.G., Norman, J.M., Kucharik, C.J., Steele, S.J., Stow, T.K. (1997) Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. Journal of Geophysical Research-Atmospheres 102, 29029–29041.

Harden, J.W., O'Neill, K.P., Trumbore, S.E., Veldhuis, H., Stocks, B.J. (1997) Moss and soil contributions to the annual net carbon flux of a maturing boreal forest. Journal of Geophysical Research-Atmospheres 102, 28805–28816.

Hart, S.A., Chen, H.Y.H. (2008) Fire, logging, and overstory affect understory abundance, diversity, and composition in boreal forest, Ecological Monographs. ESA, pp. 123–140.

Howard, E.A., Gower, S.T., Foley, J.A., Kucharik, C.J. (2004) Effects of logging on carbon dynamics of a jack pine forest in Saskatchewan, Canada. Global Change Biology 10, 1267–1284.

Hunt, S.L., Gordon, A.M., Morris, D.M. (2010) Carbon Stocks in Managed Conifer Forests in Northern Ontario , Canada. Silva Fennica 44, 563–582.

Husch, B., Beers, T.W., Kershaw, J.A. (2003) Forest Mensuration. John Wiley & Sons, Inc., New Jersey.

IPCC (2003) Good practice guidance for land use, land-use change and forestry. Special Report, Inter-Governmental Panel on Climate Change. Institute for Global Environmental Strategies for the IPCC, Hayama, Japan.

Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., Johnson, D.W., Minkkinen, K., Byrne, K.A. (2007) How strongly can forest management influence soil carbon sequestration? Geoderma 137, 253–268.

Johnson, D.W., Curtis, P.S. (2001) Effects of forest management on soil C and N storage: meta analysis. Forest Ecology and Management 140, 227–238.

Kashian, D.M., Romme, W.H., Tinker, D.B., Turner, M.G., Ryan, M.G. (2006) Carbon storage on landscapes with stand-replacing fires. Bioscience 56, 598–606.

Kasischke, E.S., Christensen, N.L., Stocks, B.J. (1995) Fire, Global Warming, and the Carbon Balance of Boreal Forests. Ecological Applications 5, 437–451.

Khomik, M., Arain, M.A., McCaughey, J.H. (2006) Temporal and spatial variability of soil respiration in a boreal mixedwood forest. Agricultural and Forest Meteorology 140, 244–256.

Krause, H. (1998) Forest floor mass and nutrients in two chronosequences of plantations: Jack pine vs. black spruce. Canadian Journal of Soil Science 78, 77–83.

Krinner, G., Viovy, N., de Noblet-Ducoudre, N., Ogee, J., Polcher, J., Friedlingstein, P., Ciais, P., Sitch, S., Prentice, I.C. (2005) A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system. Global Biogeochemical Cycles 19.

Kull, S., Rampley G., J., Morken S., Metsaranta J., M., Neilson E., T., Kurz W. A. (2011) Operational-scale carbon budget model of the Canadian forest sector (CBM-CFS3) version 1.2: user's guide. 2011, Northern Forestry Centre.

Kurz, W.A., Apps, M.J. (1996) Retrospective assessment of carbon flows in Canadian boreal forests, in: Apps, M.J., Price, D.T. (Eds.). Springer-Verlag, Heidelberg, pp. 173–183.

Laganière, J., Paré, D., Bergeron, Y., Chen, H.H., Brassard, B., Cavard, X. (2013) Stability of Soil Carbon Stocks Varies with Forest Composition in the Canadian Boreal Biome. Ecosystems, 1–14.

Lambert, M.C., Ung, C.H., Raulier, F. (2005) Canadian national tree aboveground biomass equations. Canadian Journal of Forest Research 35, 1996–2018.

MacLean, D.A., Erdle, T.A., MacKinnon, W.E., Porter, K.B., Beaton, K.P., Cormier,G., Morehouse,S., and Budd,M. (2001) The spruce budworm decision support system: Forest protection planning to sustain long-term wood supply. Canadian Journal of Forest Research 31, 1742-1757.

Martin, J.L., Gower, S.T., Plaut, J., Holmes, B. (2005) Carbon pools in a boreal mixedwood logging chronosequence. Global Change Biology 11, 1883–1894.

Mathys, A., Black, T. A., Nesic, Z., Nishio, G., Brown, M., Spittlehouse, D. L., Fredeen, A. L., Bowler, R., Jassal, R. S., Grant, N. J., Burton, P. J., Trofymow, J. A., and Meyer, G. (2012) Carbon balance of apartially harvested mixed conifer forest following mountain pine beetle attack and its comparison to a clear-cut. Biogeosciences 10, 5451-5463.

McGill, M.B., Figueiredo, C.T. (1993) Soil sampling and methods of analysis, in: Carter, M.R. (Ed.), Canadian Society of Soil Science, Lewis, Boca Raton, pp. 209–211.

Micales, J.A., Skog, K.E. (1997) The decomposition of forest products in landfills. International Biodeterioration & Biodegradation 39, 145–158.

Moroni, M.T., Shaw, C.H., Otahal, P. (2010) Forest carbon stocks in Newfoundland boreal forests of harvest and natural disturbance origin I: field study. Canadian Journal of Forest Research 40, 2135–2145.

Nalder, I.A., Wein, R.W. (1999) Long-term forest floor carbon dynamics after fire in upland boreal forests of western Canada. Global Biogeochemical Cycles 13, 951–968.

Neff, J.C., Harden, J.W., Gleixner, G. (2005) Fire effects on soil organic matter content, composition, and nutrients in boreal interior Alaska. Canadian Journal of Forest Research 35, 2178–2187.

Pan, Y.D., Birdsey, R.A., Fang, J.Y., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S.L., Rautiainen, A., Sitch, S., Hayes, D. (2011) A Large and Persistent Carbon Sink in the World's Forests. Science 333, 988–993.

Pedlar, J.H., Pearce, J.L., Venier, L.A., McKenney, D.W. (2002) Coarse woody debris in relation to disturbance and forest type in boreal Canada. Forest Ecology and Management 158, 189–194.

Pregitzer, K.S., Euskirchen, E.S. (2004) Carbon cycling and storage in world forests: biome patterns related to forest age. Global Change Biology 10, 2052–2077.

R Core Team (2012) R: A language and environment for statistical computing, R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Rapalee, G., Trumbore, S.E., Davidson, E.A., Harden, J.W., Veldhuis, H. (1998) Soil carbon stocks and their rates of accumulation and loss in a boreal forest landscape. Global Biogeochemical Cycles 12, 687–701.

Ruess, R.W., Vancleve, K., Yarie, J., Viereck, L.A. (1996) Contributions of fine root production and turnover to the carbon and nitrogen cycling in taiga forests of the Alaskan interior. Canadian Journal of Forest Research 26, 1326–1336.

Sathre, R., O'Connor, J. (2010) Meta-analysis of greenhouse gas displacement factors of wood product substitution. Environmental Science & Policy 13, 104–114.

Senici, D., Chen, H.Y.H., Bergeron, Y., Cyr, D. (2010) Spatiotemporal Variations of Fire Frequency in Central Boreal Forest. Ecosystems 13, 1227–1238.

Shorohova, E., Ignatyeva, O., Kapitsa, E., Kauhanen, H., Kuznetsov, A., Vanha-Majamaa, I. (2012) Stump decomposition rates after clear-felling with and without prescribed burning in southern and northern boreal forests in Finland. Forest Ecology and Management 263, 74–84.

Shrestha, B.M., Chen, H.Y.H. (2010) Effects of stand age, wildfire and clearcut harvesting on forest floor in boreal mixedwood forests. Plant and Soil 336, 267–277.

Soil Classification Working Group (1996) The Canadian system of soil classification, Agriculture and Agri-Food Canada Publication 1646. Ottawa, Ontario, Canada.

SP SS (2001) SPSS for Windows, Rel. 11.0.0. Chicago: SPSS Inc.

Steele, S.J., Gower, S.T., ogel, C.S., Norman, J.M. (1997) Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. Tree Physiology 17, 577–587.

Stinson, G., Kurz, W.A., Smyth, C.E., Neilson, E.T., Dymond, C.C., Metsaranta, J.M., Boisvenue, C., Rampley, G.J., Li, Q., White, T.M., Blain, D. (2011) An inventory-based analysis of Canada's managed forest carbon dynamics, 1990 to 2008. Global Change Biology 17, 2227–2244.

Sturtevant, B.R., Bissonette, J.A., Long, J.N., Roberts, D.W. (1997) Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. Ecological Applications 7, 702–712.

Taylor, A.R., Chen, H.Y.H. (2011) Multiple successional pathways of boreal forest stands in central Canada. Ecography 34, 208–219.

Taylor, A.R., Wang, J.R., Chen, H.Y.H. (2007) Carbon storage in a chronocequence of red spruce (*Picea rubens*) forest in central Nova Scotia, Canada. Canadian Journal of Forest Research 37, 2260–2269.

Taylor, K.C., Arnup, R.W., Meredith, M.P., Parton, W.J., Nieppola, J. (2000) Field Guide to Forest Ecosystems of Northeastern Ontario 2 edn. NEST Field Guide FG-01, Northeast Science and Technology, Ontario Ministry of Natural Resources, Timmins, Ontario, Canada.

Tinker, D.B., Knight, D.H. (2001) Temporal and spatial dynamics of coarse woody debris in harvested and unharvested lodgepole pine forests. Ecological Modelling 141, 125–149.

Walker, L.R., Wardle, D.a., Bardgett, R.D., Clarkson, B.D. (2010) The use of chronosequences in studies of ecological succession and soil development. Journal of Ecology 98, 725–736.

Wardle, D.A., Walker, L.R., Bardgett, R.D. (2004) Ecosystem properties and forest decline in contrasting long-term chronosequences. Science 305, 509–513.

Weber, M.G., Flannigan, M.D. (1997) Canadian boreal forest ecosystem structure and function in a changing climate: impact on fire regimes, pp. 145–166.

Weir, J.M.H., Johnson, E.A., Miyanishi, K. (2000) Fire frequency and the spatial age mosaic of the mixed-wood boreal forest in western Canada. Ecological Applications 10, 1162–1177.

Wirth, C., Schulze, E.D., Luhker, B., Grigoriev, S., Siry, M., Hardes, G., Ziegler, W., Backor, M., Bauer, G., Vygodskaya, N.N. (2002) Fire and site type effects on the long-term carbon and nitrogen balance in pristine Siberian Scots pine forests. Plant and Soil 242, 41–63.

Yanai, R.D., Stehman, S.V., Arthur, M.A., Prescott, C.E., Friedland, A.J., Siccama, T.G., Binkley, D. (2003) Detecting change in forest floor carbon. Soil Science Society of America Journal 67, 1583–1593.

Yermakov, Z., Rothstein, D.E. (2006) Changes in soil carbon and nitrogen cycling along a 72-year wildfire chronosequence in Michigan jack pine forests. Oecologia 149, 690–700.

SUMMARY IN ESTONIAN
EESTIKEELNE KOKKUVÕTE

Boreaalne mets sisaldab hulgaliselt süsinikku ja mängib seetõttu globaalses süsinikuringluses olulist rolli. Muutused boreaalse metsa süsinikuringes avaldavad mõju ka globaalsele kliimale. Ajalooliselt on olnud tuli Põhja-Ameerika boreaalse metsa ökosüsteemi protsesside peamine mõjutaja. Üha suurenenud vajadus metsa bioproduktsiooni kasutamiseks on muutnud metsaraied olulise tähtsusega häiringuteguriks. Kuigi palju tööd on tehtud boreaalse metsa süsinikuvoogude kvantifitseerimisega ja modelleerimisega, on teadmistes mitmeid olulisi lünki (näiteks: surnud juurte mass, peen- (<2 mm) ja keskmiste (2–10 mm) juurte mass, kännud). Samuti on vähe koostatud kogu metsaökosüsteemi süsinikuringet käsitlevaid üldistusi ning puudub täpne ülevaade peamistest protsessidest.

Käesolevas töös on uuritud, kuidas inimtekkelised ja looduslikud häiringud (lageraie ja tulekahju) mõjutavad metsaökosüsteemi süsinikutagavara. Töö koosneb neljast artiklist. Esimeses on esitatud kirjandusülevaade boreaalse metsa süsiniku dünaamikast. Teine keskendub elustaimestiku süsiniku dünaamikale. Kolmas töö kirjeldab lagupuidu tihedust, mis on vajalik lagupuidu mahus massi arvutamiseks. Neljas töö, mis on doktoritöö põhitulemus, kirjeldab kogu metsaökosüsteemis oleva süsiniku dünaamikat noores boreaalses metsas.

Süsinik on metsaökosüsteemis jaotunud nelja põhilise struktuurikomponendi vahel: elus biomass, surnud biomass, mulla orgaaniline osa ja mineraalse mulla orgaaniline süsinik. Need komponendid jagunevad omakorda:

1. Elus biomass:
    a. igas suuruses puud ja põõsad;
    b. alustaimestik (soontaimed, samblad, samblikud);
    c. jämejuured (>10 mm);
    d. keskmised juured (2–10 mm);
    e. peenjuured (<2 mm).

2. Surnud biomass:
    a. seisvad surnud puud;
    b. kännud;
    c. seisvate surnud puude ja kändude juured;

d. surnud keskmised ja peenjuured;
e. lamav surnud puit.

3. Mulla orgaaniline horisont

4. Mineraalse mulla orgaaniline süsinik:
   a. 0–15 cm horisont;
   b. 16–30 cm horisont;
   c. 31–100 cm horisont (keskmine kõigi proovitükkide jaoks).

Pärast häiringut muutuvad loetletud komponendid erinevalt, mõjutades üksteist metsa kasvades ning süsiniku paigutumisel ühest reservuaarist teise. Süsiniku kogust hinnati kvantitatiivselt aegrea meetodil (1, 8 ja 27 aastat pärast häiringut). Koostatud üldine andmebaas annab detailse ülevaate häiringujärgse boreaalse metsa süsinikudünaamikast.

Kogu metsaökosüsteemi süsinikutagavara (KMS) muutub pärast häiringuid oluliselt, kuid süsinikutagavara pärast metsatulekahju ja lageraiet ei erine. Kogutud andmed on sarnased teiste boreaalse metsa uuringuandmetega. Pärast raiet langeb KMS 146,5 tonnilt hektaril 127,7 tonnini ja tõuseb seejärel 185,1 tonnini hektari kohta. Pärast metsapõlengut langeb KMS 133,7 tonnilt hektaril 127,4 tonnini ja tõuseb seejärel 163,6 tonnini hektari kohta. Elus biomass, orgaaniline mulla horisont ja mineraalse mulla süsinikukogused muutusid pärast häiringuid erinevalt, surnud puidu muutumine oli pärast tulekahju ja raiet sarnane. Keskmiselt moodustas mineraalse mulla süsinik 38% süsiniku kogutagavarast, järgnesid surnud puit (29%), mulla orgaaniline horisont (20%) ja elus biomass (13%). Võttes arvesse, et nähtav on kõigest pealmine osa orgaanilisest mullast, selgitati, et noortes puistutes on kogu süsinikutagavarast (maapealsed reservuaarid) pärast lageraiet nähtav vaid 20% ja pärast põlengut 33%.

Tänased metsade majandamise võtted (lageraie ja istutus või külv) Põhja-Ameerika keskosa boreaalses segametsas KMS-i negatiivselt ei mõjuta. Arvestades puittoodete kogu elutsükli ja tooraine asenduse mõju (puidu kasutus betooni ja metalli asemel, mis omavad oluliselt suuremat süsiniku jalajälge), leiti, et lageraie põhjustab atmosfäärist suurema süsiniku netosidumise kui looduslik häiring. Uurimuse tulemused näitavad, et süsinikubilansi täpseks kirjeldamiseks on vaja arvesse võtta kõik süsinikukogused vastavalt selle paiknemisele metsaökosüsteemi eri osades.

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I

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SPECIAL FEATURE: REVIEW

Approaches for forest disturbances studies: natural variability and tree regeneration

Carbon dynamics of North American boreal forest after stand replacing wildfire and clearcut logging

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Abstract Boreal forest carbon (C) storage and sequestration is a critical element for global C management and is largely disturbance driven. The disturbance regime can be natural or anthropogenic with varying intensity and frequency that differ temporally and spatially the boreal forest. The objective of this review was to synthesize the literature on C dynamics of North American boreal forests after most common disturbances, stand replacing wildfire and clearcut logging. Forest ecosystem C is stored in four major pools: live biomass, dead biomass, organic soil horizons, and mineral soil. Carbon cycling among these pools is inter-related and largely determined by disturbance type and time since disturbance. Following a stand replacing disturbance, (1) live biomass increases rapidly leading to the maximal biomass stage, then stabilizes or slightly declines at old-growth or gap dynamics stage at which late-successional tree species dominate the stand; (2) dead woody material carbon generally follows a U-shaped pattern during succession; (3) forest floor carbon increases throughout stand development; and (4) mineral soil carbon appears to be more or less stable throughout stand development. Wildfire and harvesting differ in many ways, fire being more of a chemical and harvesting a mechanical disturbance. Fire consumes forest floor and small live vegetation and foliage, whereas logging removes large stems. Overall, the effects of the two disturbances on C dynamics in boreal forest are poorly understood. There is also a scarcity of literature dealing with C dynamics of plant coarse and fine roots, understory vegetation, small-sized and buried dead material, forest floor, and mineral soil.

Keywords Boreal forests · Carbon dynamics · Carbon pools · Clearcut logging · Wildfire

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Introduction

The boreal forest is the largest terrestrial biome (by area) in the world (Melillo et al. 1993). Its vast wetlands, forest, and permafrost form nearly a contiguous circumpolar band in the northern hemisphere, and is equivalent to roughly 50% of the carbon (C) presently in the atmosphere (Chapin et al. 2000; Gower et al. 2001). In North America, the boreal forest covers 34% of all land, occupying 412 million ha (Bourgeau-Chavez et al. 2000) and containing 66.7 Pg of C (Goodale et al. 2002). It is trans-continental, stretching from Alaska's Pacific and Arctic oceans in the west and north to the Atlantic Ocean on the eastern shore of Newfoundland and Labrador. The large C stocks in the boreal forest are the result of long periods of light during the growing season, and slow decomposition due to cold climate and poorly drained soils (Gower et al. 1997). Boreal forest C storage and sequestration is a critical element of

global C dynamics and has recently gained attention because of its importance to global warming (Harden et al. 2000; Wang et al. 2003; Howard et al. 2004; Martin et al. 2005).

The type and frequency of disturbance are key to understanding large scale boreal forest C dynamics (Banfield et al. 2002; Bond-Lamberty et al. 2004; Howard et al. 2004). Time since disturbance (TSD; e.g., stand age) is the main driver of many ecosystem functions and also of total stand C content (Pregitzer and Euskirchen 2004; Brassard and Chen 2006; Hart and Chen 2006). Ecosystem C mass varies greatly with stand age. Therefore, disturbance-driven age class distribution, affected by disturbance patterns, ultimately determines the ecosystem C balance in the boreal forest (Bhatti et al. 2002; Pregitzer and Euskirchen 2004; Magnani et al. 2007).

The primary stand replacing disturbance in North American boreal forest is wildfire (Kasischke et al. 1995; Weber and Flannigan 1997). It is the main driver of ecological processes influencing boreal forest structure and function (Bond-Lamberty et al. 2004). Human activities, such as harvesting, have historically only contributed a small fraction of the overall disturbance effects in the boreal forest (Kurz and Apps 1996). However, demand for forest products has resulted in clearcut harvesting being another major disturbance type in many areas of the boreal forest (McRae et al. 2001; Bergeron et al. 2004). Both these disturbances vary greatly in intensity and frequency. An understanding of how ecosystem C dynamics will respond to clearcut harvesting relative to wildfire is critical in understanding future C budgets of the boreal forest.

There are several reviews concerning the effects of forest age on C dynamics in forest ecosystems (e.g., Pregitzer and Euskirchen 2004), C allocation in different pools (e.g., Litton et al. 2007), and effects of climate change, CO_2 fertilization and N deposition on C dynamics (Hyvönen et al. 2007; Millard et al. 2007). Some focused on individual C pools, like coarse woody debris (Laiho and Prescott 2004) or soil (Lal 2005). However, to our knowledge, no review has examined all major C pools of the boreal forest and compared their dynamics after fire and harvesting.

In this review, we will focus on the effects of stand replacing disturbances on C storage and sequestration in boreal ecosystems. First, we describe forest C dynamics in different live biomass components. Then, we examine dead biomass C dynamics followed by forest floor C dynamics and mineral soil C dynamics. Finally, we investigate the differences between stand replacing forest fire and clearcut harvesting. We focus on literature from boreal North American forests that reports C mass, but, when necessary, studies from other ecosystems are included to better illustrate mechanisms that influence C dynamics.

Carbon flow in the ecosystem

Forest ecosystems are often divided into four major C pools that respond differently to disturbances: (1) live vegetation (above and below ground), (2) dead vegetation (snags, down woody debris, and stumps), (3) organic soil horizons (forest floor), and (4) mineral soil. Those pools are connected and transfers among pools (C allocation) inside the ecosystem occur as a forest matures (Pregitzer and Euskirchen 2004). Different C pools contain varying amounts of C and change uniquely throughout succession. C pool change along stand development is affected by many biotic and abiotic factors such as species composition, water and nutrient availability, disturbance history and climate (e.g., growing season length, temperature, and precipitation) (Banfield et al. 2002; Hyvönen et al. 2007; Litton et al. 2007).

Live biomass

Boreal forest live vegetation is mostly comprised of overstory and under-story trees, shrubs, and ground vegetation, including both aboveground and belowground (roots) components.

Trees

Following a stand replacing disturbance, biomass C accumulates slowly at first then more rapidly before reaching a maximum, after which C accumulation slows (Fig. 1). This type of growth dynamics has been observed over a wide range of forest ecosystems (Wardle et al. 2004) and is supported by several C dynamics studies in boreal (e.g.,

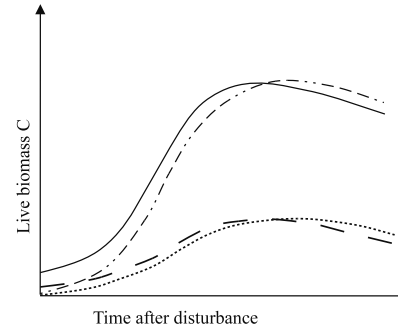

Fig. 1 Conceptual C dynamics of aboveground tree (*dash-dot line*) and root (*fine dotted line*) after fire and clearcut logging, for trees (*solid line*) and roots (*broken line*)

Martin et al. 2005) and near boreal (Rothstein et al. 2004; Yermakov and Rothstein 2006) forest regions.

The biomass accumulation is dependent on disturbance type. After a stand replacing fire that kills all live vegetation, biomass accumulation in both roots and shoots of vegetation will start from zero level (Fig. 1a). By contrast, after clearcut harvesting, biomass accumulation may be somewhat above the zero level due to residual vegetation (Fig. 1b; Seedre and Chen 2010). Therefore, post-harvest sites, when all other conditions are similar, can start developing earlier and therefore may reach maximum biomass stage sooner. The rate of C accumulation is dependent on site quality, more productive forests accumulate C faster and may reach the production peak earlier than less productive forests (Chen and Popadiouk 2002). In addition, it has been proposed that the decline phase may be more rapid in more productive forests (Chen and Popadiouk 2002).

Major causes of the decline in C accumulation in even aged forests are still unclear (Smith and Long 2001; Ryan et al. 2004). Several mechanisms have been suggested, including declining C assimilation and increased respiration, decreased soil nutrient availability (Ryan et al. 1997), and successional changes in species composition from more productive to less productive species and increased susceptibility to insect and/or wind damage (Paré and Bergeron 1995; Cavard et al. 2010). Another possible reason for age-related decline in the boreal forest is the accumulation of organic matter in the forest floor (litter–fermenting–humified, or LFH layer). A thick LFH layer contributes to soil cooling and restricts nutrient mineralization and uptake by plants (Gower et al. 1996; Murty et al. 1996; Prescott et al. 2000). Also, large amounts of nutrients in the LFH layer are in complex organic molecules and not readily accessible to plants (Prescott et al. 2000), resulting in reduced productivity. By contrast, Ryan et al. (2004) found that neither nutrient limitation nor decreased photosynthetic capacity is responsible for the decline in productivity. They proposed that decline is mostly caused by decreased canopy C gain and a shift in partitioning of sequestered C to belowground biomass and foliage respiration. A study by Smith and Long (2001) suggests that the age-related decline in C assimilation is a population phenomenon. They reported that, even if only in some sites, the age-related decline might be related to nutrient limitations, while more often it is due to mechanical abrasion because of physical interaction between individual tree crowns. In an interregional study of boreal, temperate, and tropical biomes using long-term chronosequences, Wardle et al. (2004) found the biomass decline at the late stage of stand development was associated with an increase in the substrate nitrogen to phosphorus ratio, indicating increasing phosphorus limitation over time. These authors further concluded that the maximal biomass phase during succession cannot be maintained in the long-term absence of major disturbance in forested ecosystems. It appears that multiple mechanisms can affect productivity decline including physical (mechanical), chemical (nutrients and their stoichemical compositions), and biological (canopy and understory succession) causes.

While stand live biomass declines, old-growth forests may continue to be C sinks (Malhi et al. 2004; Luyssaert et al. 2008). This appears to be a result of nitrogen deposition, higher temperature and higher CO_2 concentration in atmosphere (Spiecker 1999; Van Oijen et al. 2004; Hyvönen et al. 2007). Human-induced changes in the atmosphere has been shown by numerous studies to stimulate tree growth (reviewed by Medlyn et al. 2001; Norby et al. 2005). However, most of this sequestered C, including soil C, will be released if forests experience stand-replacing disturbances (Luyssaert et al. 2008).

While following a general sigmoidal pattern, C accumulation differs significantly between forest stand types (Gower et al. 1997) (Table 1). It has been found that aboveground C stocks and NPP can be greater in deciduous (*Populus tremuloides*) boreal forest compared with evergreen boreal (*Pinus banksiana, Picea mariana*) forests (Gower et al. 1997; Cavard et al. 2010). It is unclear why this is happening, one proposed explanation being the greater light use efficiency of deciduous forests and fewer environmental constraints on their photosynthesis (Gower et al. 1997). It has been hypothesized that mixed-wood stands have higher productivity compared with single species stands (Chen and Popadiouk 2002). Results of some studies have fully supported this hypothesis in the west boreal region, (MacPherson et al. 2001; Martin et al. 2005), partially supported it in the central boreal (Brassard et al. 2008), but do not support it in the eastern boreal region (Cavard et al. 2010). The different findings from the west to central and eastern boreal forests may be attributable to the fact the potential niche complimentarity effect between deciduous aspen and evergreen conifers was less or not realized in the eastern region where frequent spruce budworm outbreaks selectively kill large-sized balsam fir and spruce trees.

As it is the most abundant tree species in the boreal forest, black spruce (*Picea mariana* (Mill.) forests have received most attention among all boreal forest types (Gower et al. 1997) (Table 1). It has been found that soil drainage affects C dynamics (Wang et al. 2003; Grant 2004). Boreal black spruce forests in upslope stands had accumulated almost three times more wood C compared with stands in lowland areas (Grant 2004). Higher productivity was attributed to decreased soil moisture with better soil aeration (Wang et al. 2003), higher soil temperatures and higher soil nutrient availability (Grant 2004).

Table 1 C pools in the North American boreal forest of different location, forest type, moisture regime, age and origin

Reference	Location	Forest type	Moisture regime	Age	Origin	C pool (Mg C ha^{-1})			
						Live biomass	Dead wood	Forest floor	Mineral soil
Bond-Lamberty et al. (2004)	Manitoba	Black spruce	Dry site	2–130	Fire		5.0–177.6		
			Wet site	2–130	Fire		1.4–94.1		
Boulanger and Sirois (2006)	Quebec	Black spruce		4–29	Fire		2.9–13.8		
Fleming and Freedman (1998)	New Brunswick	Hardwood	Dry site	55–60	Fire	74.9–92.7	7.8–11.2	12.1–23.2	
		Mixedwood	Dry site	105	Fire	73.2	14.1	18.1	
		Coniferous	Dry site	75–95	Fire	57.1–71.0	23.7–36.9	22.9	
		Black spruce	Dry site	3–21	Harvest	0.33–29.9	0.14–16.9	15.4–31.1	
Fredeen et al. (2005)	British Columbia	Coniferous		0–20	Harvest	42	13	27	112
				0–20	Harvest	49	9	29	106
				151–250	Fire	195	35	78	115
				151–250	Fire	149	31	35	110
Gower et al. (1997)	Saskatchewan	Trembling aspen		67		93.3[a]			36.0
		Black spruce		115		49.2			390.4
		Jack pine		25–65	Fire	12.3–34.6			20.2–14.2
	Manitoba	Trembling aspen		53		57.0			97.2
		Black spruce		155		57.2			418.4
		Jack pine		25–63	Fire	7.8–29.0			25.8–28.4
Howard et al. (2004)	Saskatchewan	Jack pine		0–29	Harvest	1.2–24.4[b]	2.0–7.1	10.9–26.9	22.0–32.1
				79	Fire	38.7	3.2	8.6	20.9
Manies et al. (2005)	Manitoba	Black spruce		5–53	Fire		7.0–14.8		
Martin et al. (2005)	Manitoba	Mixedwood		11–30	Harvest	16.0–32.7	3.0–15.6	31.0–43.8	46.2–51.5
				65	Fire	60.2	9.1	24.9	53.0
Nalder and Wein (1999)	Saskatchewan	Jack pine		16–111	Fire	8.1–84.4[c]		7–21	
	Alberta/Northwest Territories	Jack pine		16–135	Fire	14.0–77.4		10–24	
	Manitoba	Jack pine		30–82	Fire	21.1–39.2		8–18	
	Saskatchewan	Trembling aspen		36–132	Fire	20.1–117.3		22–37	
	Alberta/Northwest Territories	Trembling aspen		14–149	Fire	5.0–83.1		14–46	
	Manitoba	Trembling aspen		28–112	Fire	15.0–82.4		15–31	
O'Connell et al. (2003a)	Saskatchewan	Black Spruce							
Rapalee et al. (1998)	Manitoba	Jack pine	Dry site	13–90+	Fire			0–9	0–37
		Black spruce	Moderate	13–90+	Fire			10–44	96–127
		Black spruce	Imperfect	13–90+	Fire			8–48	153–197
		Black spruce	Wet site	13–90+	Fire			7–42	117–143
Seedre and Chen (2010)	Northern Ontario	Mixedwood	Dry site	1–203	Fire	0–109.2			
		Mixedwood	Dry site	1–27	Harvest	8.7–51.8			
Taylor et al. (2008)	Nova Scotia	Red spruce		1–140	Harvest	8.31–120.7	8.1–32.0	18.9–47.1	51.4
Wang et al. (2003)	Manitoba	Black spruce	Dry site	3–151	Fire	1.3–83.3	10.3–96.0		
			Wet site	3–151	Fire	0.6–37.4	12.6–77.4		

[a] Dead biomass

[b] Total live biomass

[c] Aboveground biomass only

Boreal black spruce forests are typically covered by a continuous layer of bryophytes, commonly by feather mosses on dry sites and *Sphagnum* mosses on wet sites. While stands with feather moss cover have significantly higher total NPP (O'Connell et al. 2003a), they also have a significantly greater heterotrophic respiration rate than the stands with *Sphagnum* ground cover (O'Connell et al. 2003b). However, when bryophyte production is compared, *Sphagnum* is much more productive (Bisbee et al. 2001).

Fleming and Freedman (1998) reported that natural hardwood-dominated stands (55–60 years) have more C in live woody biomass than mixed-species (105 years) or conifer-dominated stands (75–95 years) (Table 1). However, conifer-dominated stands might have less C in live tree biomass due to the increased mortality of balsam fir and black spruce due to an infestation of spruce budworm (Fleming and Freedman 1998).

Understory vegetation

The C dynamics of understory vegetation (shrubs, herbs, mosses, lichens, and understory trees) is largely influenced by climate, soil type, stand age, overstory compositions, and disturbances (Hart and Chen 2006, 2008). Understory vegetation biomass is usually small immediately after stand replacing fire, but increase rapidly afterwards (Hart and Chen 2006, 2008; Seedre and Chen 2010). Similarly, after clearcutting, understory vegetation experiences dramatic changes in light availability and changes in species composition occur, leading to a change in biomass. More biomass C in understory vegetation is expected in clearcuts than burnt sites in early stages of stand development because stand-replacing fires tend to kill this layer, whereas logging does so only partially (Fig. 2).

The proportion of biomass in the understory may be considerable in the early stages of forest succession when it is the major living vegetation component. Later in succession, especially after canopy closure, understory share of total stand biomass decreases, eventually forming only a minor part in mature forests (Fleming and Freedman 1998; Seedre and Chen 2010). Although a small fraction of total biomass, bryophyte and understory vegetation production can equal to or exceed overstory production (Gower et al. 1997, 2001; Bisbee et al. 2001; O'Connell et al. 2003a). O'Connell et al. (2003a) found that, in mature black spruce forests with *Sphagnum* as the ground cover bryophyte, understory NPP was 51% of the total NPP (overstory, understory, bryophytes, and belowground). Another study from same area found that bryophytes accounted for 68% of the average overstory aboveground NPP (Bisbee et al. 2001).

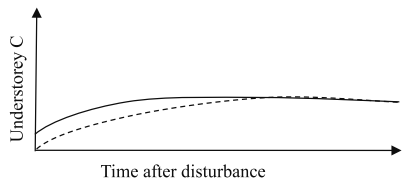

Fig. 2 Conceptual understory C dynamics after fire (*dotted line*) and clearcut logging (*solid line*)

Roots

Depending on their size and function, roots can be divided into two distinct classes: coarse and fine (Ouimet et al. 2008). Coarse roots are a significant C pool and can account 8–37% of total biomass of the tree species found in North America (Jenkins et al. 2003). Fine roots, often classified as roots <2 mm in diameter (Vogt et al. 1996), are responsible for nutrient and water uptake; they constitute a small fraction of total C pool but are a significant part of total forest production (Nadelhoffer and Raich 1992; Fahey and Hughes 1994; Ruess et al. 2003). However, classifying fine roots just by size is inadequate due to the variability of fine root dynamics, and recognizing this is required to better estimate their C dynamics (Gaudinski et al. 2001).

Coarse roots

Coarse roots, those that have undergone secondary thickening, provide structural support for aboveground components of trees, and are also highly important for nutrient storage and transport (Steele et al. 1997; Ouimet et al. 2008). Coarse root C accumulation closely follows aboveground C accumulation—it increases with time and slows at stand maturity, peaks and thereafter remains relatively constant or declines slightly (Cairns et al. 1997; Li et al. 2003; Bond-Lamberty et al. 2004; Peichl and Arain 2006; Ouimet et al. 2008). Coarse roots have small NPP compared with fine roots. In the boreal forest, coarse root NPP may be only 6% of total ecosystem NPP (Li et al. 2003), whereas their biomass is often more than 18% of total ecosystem biomass (Vogt et al. 1996).

Mostly due to the difficulties of sampling, knowledge of root C accumulation and distribution is limited and root C dynamics data are scarce compared with aboveground C components. Due to the strong relationship between tree aboveground and belowground components, root C mass is mostly estimated using root:shoot ratios (linear allometry) (Mokany et al. 2006). The root:shoot ratio is dynamic and is affected by various biotic and abiotic factors that vary spatially and temporally (Mokany et al. 2006; Brassard et al. 2009; Yuan and Chen 2010). A review by Cairns

et al. (1997) found that aboveground biomass explains 83% of variation in root biomass. It is also possible to estimate root biomass using allometric non-linear equations (e.g., power function) that can result even greater predictive power (93%) than root:shoot ratios (78%) (Mokany et al. 2006). However, although a single equation for all forest types would be convenient, the predictive power of vegetation type specific root:shoot ratios is more accurate and should be used instead (Mokany et al. 2006).

Litton et al. (2003) and Mokany et al. (2006) proposed that higher tree density and increasingly coarse soil texture were related to greater C allocation to roots, likely due to competition for nutrients and water. As trees grow bigger in size, they allocate significantly more C to aboveground parts than to roots (Litton et al. 2003; Mokany et al. 2006). Moreover, increasing precipitation resulted in a decrease of root biomass C relative to aboveground C (Schenk and Jackson 2002). Notably, limitations of nutrients and water were found to influence trees to allocate more biomass C to fine roots (Chen et al. 2002; Campbell et al. 2004). This is likely because plants adjust to nutrient and water limitations by allocating new biomass to organs that are responsible for obtaining the limiting resources (Marschner 1995; Hermans et al. 2006).

Fine roots

Carbon dynamics in fine roots is a poorly understood aspect of plant C dynamics. The C dynamics in fine roots differ from that of other tree components (Cannell and Dewar 1994; Litton et al. 2003, 2007). The majority of fine roots in boreal forests are found in the LFH layers, above the mineral soil (Steele et al. 1997; Brassard et al. 2011). Fine roots are highly dynamic; growing, dying, and decomposing continuously throughout the growing season and contribute to soil organic carbon (SOC) due to root senescence (Trumbore and Gaudinski 2003). Fine root biomass C accumulation is strongly affected by latitude, temperature, soil conditions and precipitation and varies with life-history traits of trees (Yuan and Chen 2010). Different studies have reported different fine root accumulation patterns in boreal forests. The majority of the literature suggests that fine root biomass increases rapidly after stand initiation and reaches maximum at canopy closure or stand maturity (Bond-Lamberty et al. 2004; Claus and George 2005; Peichl and Arain 2006; Yanai et al. 2006; Brassard et al. 2009). Site characteristics and species composition over time seem to determine whether fine root biomass subsequently remains stable or decreases (reviewed in Brassard et al. 2009). A meta-analysis by Yuan and Chen (2010) shows that fine root biomass in broad-leaved stands increased until 70 years and in conifer stands until 90 years and declined thereafter.

Coniferous forests allocate higher proportion of biomass to fine root production than broadleaved forests, especially in boreal forests where low soil fertility, in particular nitrogen, and soil temperature limit tree growth (Shaver et al. 1992; Gower et al. 1997; Steele et al. 1997; Ruess et al. 2006). Lower nutrient availability in conifer stands results in greater allocation to roots to better access nutrients (Hermans et al. 2006; Ruess et al. 2006). This is supported by Chen et al. (2002) who reported that, on more productive sites, trees allocated more C to woody components, whereas on less productive sites, more C is allocated to fine roots and foliage.

The share of fine root biomass of overall tree biomass is small (often <3%), but fine roots are biologically very active and their share of total forest NPP is large and can even exceed litterfall (Nadelhoffer and Raich 1992; Fahey and Hughes 1994; Vogt et al. 1996; Cairns et al. 1997). Jackson et al. (1997) found that as much as 33% of global NPP is used for fine root production. Similarly, Li et al. (2003) showed that fine root NPP in the boreal forests of the northern Canadian Prairie Provinces is 40% of total ecosystem NPP. Moreover, Ruess et al. (2003) found that annual fine root production in interior Alaska constitutes as much as 56% of total stand production. However, Strand et al. (2008) reported that fine root biomass turnover is systematically overestimated as short-term minirhizotron studies underestimate the residence time of fine roots. Using isotopic estimates, Matamala et al. (2003) also found that estimates of fine root production and turnover have been previously overestimated. Therefore, fine roots might not comprise as large a share of overall NPP as has been suggested.

Accurate estimation of total fine root biomass is complicated as large proportion of fine roots are very fine, with diameters smaller than 0.35 mm (Ruess et al. 2003, 2006). Methods like sequential coring, minirhizotrons or rhizotrons, litter bags, root screens and in-growth root cores are commonly used but suffer from several problems, such as inability to capture roots representatively due to high spatial and temporal variability of root systems and high level of introduced disturbance (Fahey and Hughes 1994; Vogt et al. 1998). For example, Ruess et al. (2003) carefully re-estimated fine root biomass in area studied earlier and found fine root biomass was five times greater than previously reported. Fahey and Hughes (1994) found that in situ screens captured 83% of fine root mass compared to in-growth cores and, when using results from in situ screen with a correction factor, the results were 20–30% lower compared to coring and in-growth core estimates. Therefore, many previous studies may have underestimated fine root biomass, and more accurate methods (e.g., radiocarbon tracers) may need to be applied.

Dead biomass

Dead biomass is comprised of leaf litter, dead wood and dead roots. The C dynamics of dead biomass reflect its rate of decomposition and accrual from live biomass. Decomposition of dead biomass is strongly influenced by its chemical and physical characteristics, which vary greatly with species and are influenced by factors such as temperature, moisture and aeration (Laiho and Prescott 2004), proximity to the soil and the standing or fallen position of the dead material (Vogt et al. 1996). Wood decomposition tends to decrease with decreasing mean annual temperature (Yatskov et al. 2003). Decomposition of dead biomass is faster in moist warm sites compared with sites that are dry and cold. Standing dead trees (snags) decompose slower than fallen logs due to direct contact of the latter with the soil; fallen logs having higher moisture content and direct contact with wood-decomposing insects and other organisms in the soil compared to standing dead trees (Shorohova and Shorohov 2001). Generally, broad-leaved species decompose faster than conifers (Weedon et al. 2009). Boreal forests have low mean annual temperature and short growing seasons compared to forests in most other parts of the world. Therefore, heterotrophic activity is lower, causing reduced rates of C and nutrient cycling from dead biomass (Trofymow et al. 2002).

Coarse woody debris (CWD) includes recently died and decaying logs, snags (standing dead trees) and stumps generally greater than 10 cm in diameter (Harmon and Sexton 1996). The function of CWD in sediment transport, humus formation (Harmon et al. 1986) and as animal habitat (Pedlar et al. 2002; Lindbladh et al. 2007) has been well studied. The role of CWD in C cycling and its importance as a C stock has gained attention only recently (Krankina and Harmon 1995; Yatskov et al. 2003; Manies et al. 2005). CWD is also important in long-term C storage because of the slow rate of decomposition due to its low surface area and high lignin content (Harmon et al. 1986), especially in the boreal forest (Manies et al. 2005).

Coarse woody debris C accumulation in the boreal forest is significantly affected by time since disturbance and can follow several different patterns that are strongly influenced by stand species composition (Hély et al. 2000; Arseneault 2001; Brassard and Chen 2006, 2008). There can be a continuous increase of CWD mass with stand age (Hély et al. 2000), an inverse U-shaped accumulation curve (Brown and See 1981) or a U- or S-shaped curve (Sturtevant et al. 1997; Clark et al. 1998; Pedlar et al. 2002; Brais et al. 2005; Martin et al. 2005). The most common of these in the boreal forest is the U-shaped CWD accumulation curve.

The U-shaped pattern of CWD accumulation is believed to occur in post-fire stands as follows. During the early stages of forest development in post-fire stands, the pre-disturbance debris, disturbance-generated debris, and residual standing trees all contribute large amounts of CWD and the total CWD C pool size is high (Lee et al. 1997). Fire only consumes ca. 8% of pre-disturbance dead wood, another 8% being converted to charcoal (Tinker and Knight 2001). Initially after fire, the residual material declines logarithmically as CWD decomposes. Little additional dead woody material arises until regenerating stands begin to experience mortality due to self-thinning during the stem exclusion phase of stand development, after which CWD mass increases exponentially. This type of U- or S-shaped pattern has been observed in single-species stands (Sturtevant et al. 1997; Pedlar et al. 2002; Brais et al. 2005), in younger mixed-wood stands (11–65 years) of logging origin (Martin et al. 2005), as well as long chronosequences (7–201 years) of boreal mixed woods of different overstory compositions (Brassard and Chen 2008). An inverse U-shaped curve can occur when tree mortality is particularly high due to high tree density, windthrow, insects, or disease during the mid-age of the stand (Harmon et al. 1986; Feller 2003).

Logging results in different CWD dynamics from fire, generally following a U-shaped curve but with lower initial input to the CWD pool. However, if site preparation, planting/seeding, and tending result in faster stand initiation, the stands will reach the stem exclusion stage sooner (Fig. 3; Table 1). While most dead woody material remains on site after fire, after logging most large woody material has been removed.

The amount of CWD left on site also depends on harvesting method, e.g., whole tree harvest or cut-to-length, and on practices such as collection of biofuel. Those factors also determine CWD distribution on site. If advanced regeneration is present, or if planting or aerial seeding are performed after logging, new stand initiation can be faster and time to reach the stem exclusion phase of stand development may be faster than after fire, shortening the time to reach the stage of exponentially increasing CWD (Fig. 3).

It is important to distinguish between new CWD dynamics (the change caused by inputs from the latest

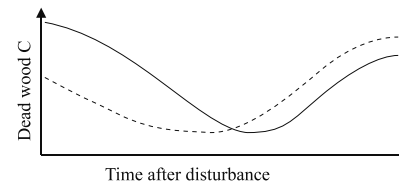

Fig. 3 Conceptual dead wood C dynamics after fire (*solid line*) and clearcut logging (*dotted line*)

stand disturbance) and the total size of the CWD pool (Ter-Mikaelian et al. 2008). Immediately after a disturbance, total CWD pool size depends on input of new CWD from the most recent disturbance and the amount of old CWD in the stand prior to the most recent disturbance. The amounts of new and old CWD are affected by stand age/stage of development when disturbance occurs. In the boreal forests, the contribution of, in particular, the old CWD snags to post-fire CWD is likely low since dead woody material is more easily consumed during typical intense crown fires.

Fire may affect a stand at any time in its life cycle, greatly altering the pre-disturbance CWD pool size and the amount of new CWD contributed from the overstory trees. Consider, for example, two 20-year-old stands of the same species composition, one established after harvesting and the other after fire. The one established after harvesting would have a relatively low amount of CWD on site due to stem removal, while the one established after fire would have relatively large amount of CWD. If both stands then burned at age 20, the one previously established following harvesting would have both small new CWD and small old CWD. The one established after fire would have small new CWD and large old CWD.

In contrast to the above example, a stand harvested during succession from shade-intolerant to -tolerant species would contain relatively large amounts of CWD from the previous intolerant overstory and would add to that with additional CWD from logging slash. These contrasting potential outcomes in CWD amounts despite similar CWD dynamics demonstrate the importance of stand history in determining total amounts of CWD, and stands ostensibly similar can vary widely in total CWD despite having very similar new CWD dynamics.

Although volume dynamics of CWD is now fairly well generalized (Brassard and Chen 2006), mass and C dynamics of CWD are still unclear since CWD wood densities differ with stand development, attributed to CWD size, species composition, and decay status (Laiho and Prescott 2004). Changes in decay class (roughly representing density) (Creed et al. 2004) are related to changes in C and N concentration, since during decomposition, mass and C in CWD are lost by leaching and C reduced by decomposition (Harmon and Sexton 1996; Krankina et al. 1999; Creed et al. 2004). Increasing decay leads to considerable decline in wood density and there is a small increase in C (also in N and P) concentration especially in late stages of decay due to relative abundance of lignin (Preston et al. 1998; Sandstrom et al. 2007). The structural integrity of the dead wood is retained as some of the more recalcitrant portions do not decompose, reducing wood density and C density (Harmon et al. 1986).

There is considerable uncertainty about the total size of the dead wood C stock. Dead wood studies often focus on CWD and other visible dead material, while because of difficulties sampling it, fine-sized debris, buried material, and dead roots (both fine and coarse) are often not studied. This hinders full characterization of the dead wood pool and its contribution to C stocks and C cycling (Manies et al. 2005). Partially and completely buried wood can comprise up to 26% of the total woody debris in older stands (Manies et al. 2005). Small debris (<5 cm diameter), which may not be sampled in surveys of CWD, can comprise up to 43% of total dead wood biomass (Hély et al. 2000). Therefore, it appears probable that many published estimates of CWD seriously underestimate the size of this C pool.

Forest floor

Many boreal forest stands have thick organic LFH layers above the mineral soil, which is often referred to as forest floor (FF) or organic soil layer. The FF comprises leaf litter, fine woody litter, and roots and may also contain substantial amounts of mineral soil mixed in from below by animals or other agents (Yanai et al. 2003a). Limited decomposition rate of organic matter in the boreal region results in an accumulation of the organic layers above the mineral soil (Harden et al. 1997). The FF is a major nutrient-rich pool and the most biologically active portion of boreal forest soils (Krause 1998). Since it is closer to the surface, FF is also more sensitive to fluctuations in temperature and moisture (Khomik et al. 2006).

Humus in the FF is made up of recalcitrant products of litter decomposition (Prescott et al. 2000). Humus formation involves microbial modification of lignin and condensation of proteins into humus precursors that are bound in humus by chemical complexation (Prescott et al. 2000). Although vegetation is unable to uptake nutrients tied up in complex humus molecules, fire releases these nutrients making them available to new vegetation or to leaching (Lecomte et al. 2006). Incorporation of humus in soil can bind C for thousands of years (Dec and Bollag 1997).

A large portion of surface organic material of FF is consumed during wildfire (Neff et al. 2005; Shrestha and Chen 2010). The proportion of FF consumed by forest fire varies greatly (15–100%) depending on fire intensity (DeBano et al. 1998; Kasischke and Bruhwiler 2002; Neff et al. 2005). Stand replacing fires are high intensity, often consuming much of the FF (Yanai et al. 2003b; Certini 2005). After fire, with regeneration, the FF starts to accumulate and increases throughout the life of a stand (Rapalee et al. 1998; Nalder and Wein 1999; Shrestha and Chen 2010) (Fig. 4). In contrast, on harvested sites, dead biomass C in the FF remains and can slightly increase with decomposition of debris from harvested trees in the first

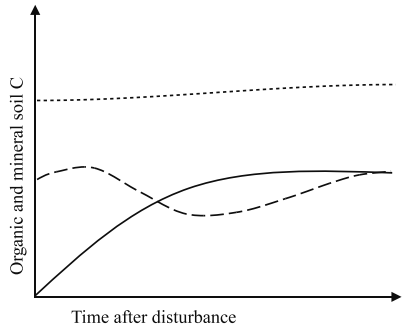

Fig. 4 Conceptual soil C dynamics in organic layer (FF) after fire (*solid line*) and after clearcut logging (*broken line*) and in mineral soil (*dotted line* for both disturbances)

few years after harvest but will later decline until there is renewed input of organic material from new stands (Shrestha and Chen 2010) (Fig. 4).

Nalder and Wein (1999) found a positive and highly significant relationship between C in FF and stand age. Synthesis of C data by Pregitzer and Euskirchen (2004) concluded that boreal forest C in the FF accumulates until stands are ca. 70 years old, after which FF C remains relatively constant or increases slowly. The relatively short fire cycles in central and western Canada (Johnson 1992; Senici et al. 2010) means that a smaller proportion of stands reach old age than in boreal eastern Canada. Generally, most nutrients bound in the FF are more regularly released by fire and become available for plants, while the longer fire return intervals in eastern Canada (Bergeron et al. 2004) allows FF to often become thicker and to accumulates C for long periods (>700 years) between fires (Lecomte et al. 2006). Prolonged absence of fire regulates C partitioning between live biomass and FF. In stands younger than 200 years, most of the ecosystem C is stored in live biomass C, but in older stands (>200 years), most of the C is in FF (Xing et al. 2005).

The C accumulation in FF is strongly influenced by stand species composition, its productivity and regional climate (Nalder and Wein 1999) (Table 1). For example, C in FF was significantly higher in aspen stands compared with pine stands in western boreal forest (Nalder and Wein 1999). However, whether broadleaf stands store generally more or less C in FF than conifers is unknown. For example, Thomas and Prescott (2000) reported smaller, and Binkley et al. (1992) reported greater, FF C under broadleaf species compared with conifers. These differences might be due to differences in species identity, fire history, and stand age rather than broadleaf–conifer differences. In addition, drainage affects FF biomass and C stock, with poorly drained soils having higher C in FF compared with well-drained soils (Rapalee et al. 1998).

Mineral soil

Carbon in mineral soil is commonly assessed up to 1 m depth where its content can be very high (Table 1). Because of its large size, any changes in soil C pools are important for total forest C storage (Siltanen et al. 1997; Medlyn et al. 2005). Even a small change in soil C could have considerable impacts on atmospheric CO_2 concentration and other greenhouse gases and, therefore, also on climate (Hossain et al. 2007). Soil C pool size is regulated by the balance between C inputs from litterfall and rhizodeposition on one hand and C released from decomposition on the other (Jandl et al. 2007). Fine roots contribute substantially more to mineral soil C and nutrient pools than aboveground litter as elements can more easily leach to mineral soil (Ruess et al. 1996). C accumulation in boreal forest soils can be explained by difference between fine root NPP and fine root turnover (Steele et al. 1997). Even with low nutrients, permafrost-dominated, or late successional ecosystems, C and presumably other nutrients cycle through fine roots at a rate of several orders of magnitude faster than through aboveground tissues (Ruess et al. 2003). Therefore, factors influencing stand species composition and growth also affect soil C storage. Total size of SOC stock is also influenced by stand age, disturbance type and intensity, climate (temperature and precipitation), soil texture, bulk density, and topography (Johnson and Curtis 2001; Bhatti et al. 2002) (Table 1).

Forest fires can affect physical, chemical, mineralogical and biological properties of mineral soil and the effects are dependent on peak temperatures and duration of fire (Certini 2005). Although immediate fire impacts are mostly limited to surface dead moss and fibric horizons, with no change in the mineral soil (Neff et al. 2005), approximately 10–15% of the heat generated can transfer downward into the mineral soil during wildfire (Raison et al. 1986). Therefore, direct effects of fire on soil organic C pool is largely dependent on fire intensity (DeBano et al. 1998).

Although fire affects forest soil in various ways, there is no clear understanding of how it influences SOC and its amounts in soil. A comprehensive synthesis of the literature by Pregitzer and Euskirchen (2004) reported that, although the soil C pool in the boreal forest is highly variable, an overall trend of increasing C pool size with increasing time since fire can be observed (Fig. 4). In one study (Bormann et al. 2008), there was a reported loss of 60% of soil C from mineral soil after fire, indicating that intense forest fire can sharply reduce mineral soil C. However, in general, there is no consistent effect of forest

fire on mineral soil C, presumably because fire effects are limited in the upper 5 cm of the soil (Johnson and Curtis 2001; Certini 2005). In a meta-analysis of 13 studies, Johnson and Curtis (2001) found no significant overall effect of fire on C in the A-horizon nor on total soil C.

Most studies on mineral soil C sample the soil up to 1 m depth. Quantifying C in deeper horizons might be largely irrelevant in C cycling calculations as this pool is neither dynamic nor large (Houghton 1995). Huang and Schoenau (1996) calculated that at depths below 1 m (1–3.2 m) in BOREAS study sites in Saskatchewan, there was an average of 60.6 Mg ha^{-1} SOC. Jobbagy and Jackson (2000) studied SOC down to 3 m depth using a meta-analysis and reported that boreal forests soils had 112, 29 and 10 Mg C ha^{-1} in soil depths of 0–1, 1–2 and 2–3 m, respectively. They also found that SOC content increased with precipitation and soil clay content and decreased with temperature. Plant types and plant functional groups (forests, shrubs, grasses), through differences in C allocation, also influence SOC distribution with depth in the soil (Jobbagy and Jackson 2000).

Differences between forest fire and logging

Harvesting has contributed only a small fraction of the total area of disturbance in the boreal forest in the past century (Kurz and Apps 1996). There are only a few studies conducted in the North American boreal forest directly comparing the effects of fire and logging on C dynamics of live vegetation (Seedre and Chen 2010), CWD (Pedlar et al. 2002; Brassard and Chen 2008), FF and soil (e.g., Smith et al. 2000; Simard et al. 2001; Leduc and Rothstein 2007; Shrestha and Chen 2010). Some studies have compared C dynamics of older natural forests developed after fire with younger managed forest regenerated after logging (e.g., Fleming and Freedman 1998; Howard et al. 2004; Fredeen et al. 2005; Martin et al. 2005)

Fire, even if it is non-stand replacing, consumes litter, small live branches, foliage, and organic soil horizons. During a fire, an immediate transfer by combustion of a portion of ecosystem C to the atmosphere takes place (Harden et al. 2000). However, the fire consumes only about 8% of dead wood at the time of fire and another 8% is converted to charcoal (Tinker and Knight 2001). Charcoal is a stable form of C that can last in forest soils for thousands of years (DeLuca and Aplet 2008).

In contrast to fire, harvesting removes live biomass from the forest. Full carbon accounting requires that the fate of carbon in harvested trees and wood products be understood. One use of harvested biomass and coarse wood debris is as bioenergy. Bioenergy is combusted, returning all the stored C back to the atmosphere (McKechnie et al. 2011). However, bioenergy allows fossil fuel use to be reduced, avoiding emissions from non-renewable fuel types. McKechnie et al. (2011) found that harvesting northern deciduous forests required about 40 years before forest regrowth balanced carbon emissions related to the biofuel production life cycle and the transfer of carbon stored in trees to the atmosphere.

A more common use of harvested woody biomass is in solid wood products and paper. Wood in these end-uses will be in use, recycled, or, when there is no other use, they will be burned (usually for energy), or placed in landfills (Chen et al. 2008). Only a fraction of C from landfills will eventually be released back to the atmosphere within 100 years making landfills a significant long-term C stock (Micales and Skog 1997). However, landfilled wood products emit half the carbon they contain as methane and this also needs to be accounted for in a full C accounting. Methane landfill can be flared (to convert it to CO_2), or captured and burned to produce energy to displace fossil fuel.

In addition to their direct role in storing C, wood replaces other types of products that usually have higher life cycle emissions. To understand the full implications of harvest on net greenhouse gas emissions, it is important to account for life cycle emissions from harvest, transportation of wood to processing plants, mill emissions, and transport of the products to distributors and consumers to determine net C budgets for harvested stands (Gower 2003). Such life cycle analyses need to be done comparatively with emissions from non-wood products that would have been used if wood were not employed. Sathre and O'Connor (2010) report an average displacement factor of 2.1 t C (i.e., there was on average a net reduction of 2.1 t C in net greenhouse gas emissions per t wood used in place of alternative building materials). Thus, a complete picture of the relative C dynamics of fire and harvest needs to include the fate of wood after it is removed from the forest.

The amount of CWD is one of the most obvious differences between wildfire and clearcut origin stands (Harmon et al. 1990; Sippola et al. 1998; Fridman and Walheim 2000; Siitonen et al. 2000; Brassard and Chen 2008). Studies in Canadian boreal mixedwoods show that recent burns consisted mostly of standing dead wood of various sizes, while recent clearcuts consisted of logs and stumps relatively small in size, while the amount and type of CWD in both clearcut and fire origin stands were highly dependent on time since disturbance (Pedlar et al. 2002; Brassard and Chen 2008).

Although stand replacing fires typically kill live trees, they only consume a fraction of the biomass (Kashian et al. 2006). Fires mostly consume litter and FF (Simard et al. 2001). After an immediate large pulse of C released to the atmosphere during the fire, C is later lost through

decomposition of dead vegetation (Kasischke et al. 1995). The rate of decomposition of standing dead trees is slow until the trees fall and make contact with the soil. At this stage, their moisture content increases and the wood becomes colonized by heterotrophs (Harmon et al. 1986; Wang et al. 2002). Dead vegetation decomposition causes greater C release than fire itself (Kashian et al. 2006). As much as three times more CO_2 can be released to the atmosphere via decomposition of dead roots and stems in the several decades following fire than during the fire (AuClair and Carter 1993). Contrary to stands that have burned, in clearcut sites most tree stems are removed and only decomposition of the material left on site will contribute to CO_2 emissions.

Various results with respect to soil C pools size between logging and fire on different ecosystems have been reported (Table 1), but there seems to be no clear trend (Fig. 4). Pumpanen et al. (2004) found that the SOC pool might increase in the long run as a result of intensive forest management. Leduc and Rothstein (2007) compared soil C and N dynamics after wildfire and clearcutting in Michigan jack pine stands and found no difference in total or labile soil C pools. However, significantly lower total and labile soil N pool and nitrification was present after wildfire, with potentially important consequences on plant growth and C acquisitions. A study from Quebec's boreal forest by Simard et al. (2001) showed that clearcutting and wildfire could have different effects on soil nutrient status, but no conclusion was reached about the effects on long-term productivity. A meta analysis by Johnson and Curtis (2001) showed that both fire and harvesting had little or no effect on soil C and N. Significant effects were related to harvest type, with saw log harvesting causing an 18% increase and whole-tree harvesting causing a 6% decrease in soil C and N pools (Johnson and Curtis 2001). For unknown reasons, the positive effect of saw log harvesting on C and N pools was restricted to conifer stands.

A review of forest management effects on mineral soil C by Jandl et al. (2007) clearly showed that forest management directly influenced C flux in the soil, with the overall effect of harvesting on soil C dependent on the degree of soil disturbance during harvesting. Smith et al. (2000) found that fire and reduced-impact harvesting (cutting with protection of tree regeneration and soils) affected soil processes of upland black spruce stands in similar ways. Despite long-term differences in stand stocking and fine root biomass, soil C, N, and P stocks and dynamics recovered to similar levels several decades after disturbance. Smith et al. (2000) highlighted the need for future studies in stands that have experienced more than one biomass removal to determine if C and nutrient stocks return to similar levels after repeated harvestings.

Conclusion

The boreal forest is a very large terrestrial C pool and it has a large influence on global C balance. Live biomass and FF increase with stand development; while the former will remain stable or even decline, the latter tends to increase continuously in later stages. Dead wood shows a U-shaped pattern with stand development. Soil C pools experience a decline immediately after disturbance and start to increase later with stand development. Large-scale logging has been carried out in the boreal forest for about five decades, and its long-term effects on C dynamics are not well understood. Several critical knowledge gaps need to be filled in order to better understand boreal forest C dynamics. These can be classified as better information on the structural makeup of the boreal forest and better estimates of C density for different ecosystem pools.

Improved forest inventory must be supported by better estimates of C density in different C pools. While all forest carbon pools are in need of study, the pools requiring most immediate attention are: (1) belowground components, especially coarse and fine roots that are the least understood aspect of C dynamics, (2) understory and bryophyte dynamics, which comprise a minor C pool, but represent a large portion of annual stand biomass production because of their fast turnover rates, (3) coarse woody debris C dynamics, which may differ from generally well-known volume dynamics, (4) fine woody debris and partially and completely buried woody debris, and (5) forest floor and mineral soil C dynamics.

Studies on C dynamics should include all C pools as it would largely advance our understanding of C allocation throughout stand development. Future research should also focus on comparing the effects of wildfire and harvesting stands with different management intensities. It is especially important to enhance the understanding of possible management effects on C cycling as human footprints through management in the boreal forest are expected to increase with society's demands for forest products and energy sources.

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References

Arseneault D (2001) Impact of fire behavior on postfire forest development in a homogeneous boreal landscape. Can J For Res 31:1367–1374

AuClair AND, Carter TB (1993) Forest wildfires as a recent source of CO_2 at northern latitudes. Can J For Res 23:1528–1536
Banfield GE, Bhatti JS, Jiang H, Apps MJ (2002) Variability in regional scale estimates of carbon stocks in boreal forest ecosystems: results from West-Central Alberta. For Ecol Manag 169:15–27
Bergeron Y, Gauthier S, Flannigan M, Kafka V (2004) Fire regimes at the transition between mixedwood and coniferous boreal forest in Northwestern Quebec. Ecology 85:1916–1932
Bhatti JS, Apps MJ, Tarnocai C (2002) Estimates of soil organic carbon stocks in central Canada using three different approaches. Can J For Res 32:805–812
Binkley D, Sollins P, Bell R, Sachs D, Myrold D (1992) Biogeochemistry of adjacent conifer and alder-conifer stands. Ecology 73:2022–2033
Bisbee KE, Gower ST, Norman JM, Nordheim EV (2001) Environmental controls on ground cover species composition and productivity in a boreal black spruce forest. Oecologia 129:261–270
Bond-Lamberty B, Wang CK, Gower ST (2004) Net primary production and net ecosystem production of a boreal black spruce wildfire chronosequence. Glob Change Biol 10:473–487
Bormann BT, Homann PS, Darbyshire RL, Morrissette BA (2008) Intense forest wildfire sharply reduces mineral soil C and N: the first direct evidence. Can J For Res 38:2771–2783
Bormann FH, Likens GE (1979) Pattern and process in a forested ecosystem. Springer, New York
Bourgeau-Chavez LL, Kasischke ES, Mudd JP, French NHF (2000) The role of fine roots in the functioning of boreal forests. In: Kasischke ES, Stocks BJ (eds) Fire, climate change and carbon cycling in the boreal forest. Ecological studies series. Springer, New York, pp 258–273
Brais S, Sadi R, Bergeron Y, Grenier Y (2005) Coarse woody debris dynamics in a post-fire jack pine chronosequence and its relation with site productivity. For Ecol Manag 220:216–226
Brassard BW, Chen HYH (2006) Stand structural dynamics of North American boreal forests. Crit Rev Plant Sci 25:115–137
Brassard BW, Chen HYH (2008) Effects of forest type and disturbance on diversity of coarse woody debris in boreal forest. Ecosystems 11:1078–1090
Brassard BW, Chen HYH, Wang JR, Duinker PN (2008) Effects of time since stand-replacing fire and overstory composition on live-tree structural diversity in the boreal forest of central Canada. Can J For Res 38:52–62
Brassard BW, Chen HYH, Bergeron Y (2009) Influence of environmental variability on root dynamics in northern forests. Crit Rev Plant Sci 28:179–197
Brassard BW, Chen HYH, Bergeron Y, Paré D (2011) Differences in fine root productivity between mixed- and single-species stands. Funct Ecol 25:238–246
Brown JK, See TE (1981) Downed dead woody fuel and biomass in the northern Rocky Mountains. General Technical Report INT-117. USDA Forest Service
Brown PM, Shepperd WD, Mata SA, McClain DL (1998) Longevity of windthrown logs in a subalpine forest of central Colorado. Can J For Res 28:932–936
Boulanger Y, Sirois L (2006) Postfire dynamics of black spruce coarse woody debris in northern boreal forest of Quebec. Can J For Res 36:1770–1780
Cairns MA, Brown S, Helmer EH, Baumgardner GA (1997) Root biomass allocation in the world's upland forests. Oecologia 111:1–11
Campbell JL, Sun OJ, Law BE (2004) Supply-side controls on soil respiration among Oregon forests. Glob Change Biol 10:1857–1869
Cannell MGR, Dewar RC (1994) Carbon allocation in trees—a review of concepts for modeling. Adv Ecol Res 25:59–104
Cavard X, Bergeron Y, Chen HYH, Paré D (2010) Mixed-species effect on tree aboveground carbon pools in the east-central boreal forests. Can J For Res 40:37–47
Certini G (2005) Effects of fire on properties of forest soils: a review. Oecologia 143:1–10
Chapin FS, Mcguire AD, Randerson J, Pielke R, Baldocchi D, Hobbie SE, Roulet N, Eugster W, Kasischke E, Rastetter EB, Zimov SA, Running SW (2000) Arctic and boreal ecosystems of western North America as components of the climate system. Glob Change Biol 6:211–223
Chen HYH, Popadiouk RV (2002) Dynamics of North American boreal mixedwoods. Environ Rev 10:137–166
Chen J, Colombo SJ, Ter-Mikaelian MT, Heath LS (2008) Future carbon storage in harvested wood products from Ontario's Crown forests. Can J For Res 38:1947–1958
Chen WJ, Chen JM, Price DT, Cihlar J (2002) Effects of stand age on net primary productivity of boreal black spruce forests in Ontario, Canada. Can J For Res 32:833–842
Clark DF, Kneeshaw DD, Burton PJ, Antos JA (1998) Coarse woody debris in sub-boreal spruce forests of west-central British Columbia. Can J For Res 28:284–290
Claus A, George E (2005) Effect of stand age on fine-root biomass and biomass distribution in three European forest chronosequences. Can J For Res 35:1617–1625
Creed IF, Webster KL, Morrison DL (2004) A comparison of techniques for measuring density and concentrations of carbon and nitrogen in coarse woody debris at different stages of decay. Can J For Res 34:744–753
DeBano LF, Neary DG, Folliott PF (1998) Fire's effect on ecosystems. Wiley, New York
Dec J, Bollag JM (1997) Determination of covalent and noncovalent binding interactions between xenobiotic chemicals and soil. Soil Sci 162:858–874
DeLuca TH, Aplet GH (2008) Charcoal and carbon storage in forest soils of the Rocky Mountain West. Front Ecol Environ 6:18–24
Eriksson E, Gillespie AR, Gustavsson L, Langvall O, Olsson M, Sathre R, Stendahl J (2007) Integrated carbon analysis of forest management practices and wood substitution. Can J For Res 37:671–681
Fahey TJ, Hughes JW (1994) Fine root dynamics in a northern hardwood forest ecosystem, Hubbard Brook Experimental Forest, NH. J Ecol 82:533–548
Feller MC (2003) Coarse woody debris in the old-growth forests of British Columbia. Environ Rev 11:135–157
Fleming TL, Freedman B (1998) Conversion of natural, mixed-species forests to conifer plantations: Implications for dead organic matter and carbon storage. Ecoscience 5:213–221
Fredeen AL, Bois CH, Janzen DT, Sanborn PT (2005) Comparison of coniferous forest carbon stocks between old-growth and young second-growth forests on two soil types in central British Columbia, Canada. Can J For Res 35:1411–1421
Fridman J, Walheim M (2000) Amount, structure, and dynamics of dead wood on managed forestland in Sweden. For Ecol Manag 131:23–36
Gaudinski JB, Trumbore SE, Davidson EA, Cook AC, Markewitz D, Richter DD (2001) The age of fine-root carbon in three forests of the eastern United States measured by radiocarbon. Oecologia 129:420–429
Goodale CL, Apps MJ, Birdsey RA, Field CB, Heath LS, Houghton RA, Jenkins JC, Kohlmaier GH, Kurz W, Liu SR, Nabuurs GJ, Nilsson S, Shvidenko AZ (2002) Forest carbon sinks in the Northern Hemisphere. Ecol Appl 12:891–899
Gower ST (2003) Patterns and mechanisms of the forest carbon cycle. Annu Rev Environ Resour 28:169–204
Gower ST, Krankina O, Olson RJ, Apps M, Linder S, Wang C (2001) Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol Appl 11:1395–1411

Gower ST, McMurtrie RE, Murty D (1996) Aboveground net primary production decline with stand age: potential causes. Trends Ecol Evol 11:378–382

Gower ST, Vogel JG, Norman JM, Kucharik CJ, Steele SJ, Stow TK (1997) Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. J Geophys Res Atmos 102:29029–29041

Grant RF (2004) Modeling topographic effects on net ecosystem productivity of boreal black spruce forests. Tree Physiol 24:1–18

Harden JS, O'Neill KP, Trumbore SE, Veldhuis H, Stocks BJ (1997) Moss and soil contributions to the annual net carbon flux of a maturing boreal forest. J Geophys Res 102:28817–28830

Harden JW, Trumbore SE, Stocks BJ, Hirsch A, Gower ST, O'Neill KP, Kasischke ES (2000) The role of fire in the boreal carbon budget. Glob Change Biol 6:174–184

Harmon ME, Ferrell WK, Franklin JF (1990) Effects on carbon storage of conversion of old-growth forests to young forests. Science 247:699–702

Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SP, Aumen NG, Sedell JR, Lienkaemper GW, Cromack K, Cummins KW (1986) Ecology of coarse woody debris in temperate ecosystems. Adv Ecol Res 15:133–302

Harmon ME, Sexton J (1996) Guidelines for measurements of woody detritus in forest ecosystems. Publication No. 20. U.S. LTER Network Office, University of Washington, Seattle

Hart SA, Chen HYH (2006) Understory vegetation dynamics of North American boreal forests. Crit Rev Plant Sci 25:381–397

Hart SA, Chen HYH (2008) Fire, logging, and overstory affect understory abundance, diversity, and composition in boreal forest. Ecol Monogr 78:123–140

Hazlett PW, Gordon AM, Sibley PK, Buttle JM (2005) Stand carbon stocks and soil carbon and nitrogen storage for riparian and upland forests of boreal lakes in northeastern Ontario. For Ecol Manag 219:56–68

Hély C, Bergeron Y, Flannigan WD (2000) Coarse woody debris in the southeastern Canadian boreal forest: composition and load variations in relation to stand replacement. Can J For Res 30:674–687

Hermans C, Hammond JP, White PJ, Verbruggen N (2006) How do plants respond to nutrient shortage by biomass allocation? Trends Plant Sci 11:610–617

Hossain MF, Zhang Y, Chen WJ, Wang JX, Pavlic G (2007) Soil organic carbon content in northern Canada: a database of field measurements and its analysis. Can J Soil Sci 87:259–268

Houghton RA (1995) Changes in the storage of terrestrial carbon since 1850. In: Lal R, Kimble E, Levine E, Stewart BA (eds) Soil and global change. CRC & Lewis, Boca Raton, pp 45–65

Howard EA, Gower ST, Foley JA, Kucharik CJ (2004) Effects of logging on carbon dynamics of a jack pine forest in Saskatchewan, Canada. Glob Change Biol 10:1267–1284

Huang WZ, Schoenau JJ (1996) Forms, amounts and distribution of carbon, nitrogen, phosphorus and sulfur in a boreal aspen forest soil. Can J Soil Sci 76:373–385

Hyvönen R, Agren GI, Linder S, Persson T, Cotrufo MF, Ekblad A, Freeman M, Grelle A, Janssens IA, Jarvis PG, Kellomaki S, Lindroth A, Loustau D, Lundmark T, Norby RJ, Oren R, Pilegaard K, Ryan MG, Sigurdsson BD, Stromgren M, van Oijen M, Wallin G (2007) The likely impact of elevated [CO_2], nitrogen deposition, increased temperature and management on carbon sequestration in temperate and boreal forest ecosystems: a literature review. New Phytol 173:463–480

Jackson RB, Mooney HA, Schulze ED (1997) A global budget for fine root biomass, surface area, and nutrient contents. Proc Natl Acad Sci USA 94:7362–7366

Jandl R, Lindner M, Vesterdal L, Bauwens B, Baritz R, Hagedorn F, Johnson DW, Minkkinen K, Byrne KA (2007) How strongly can forest management influence soil carbon sequestration? Geoderma 137:253–268

Jenkins JC, Chojnacky DC, Heath LS, Birdsey RA (2003) National-scale biomass estimators for United States tree species. For Sci 49:12–35

Jobbagy EG, Jackson RB (2000) The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecol Appl 10:423–436

Johnson DW, Curtis PS (2001) Effects of forest management on soil C and N storage: meta analysis. For Ecol Manag 140:227–238

Johnson EA (1992) Fire and vegetation dynamics—studies from the North American boreal forest. Cambridge University Press, Cambridge

Kashian DM, Romme WH, Tinker DB, Turner MG, Ryan MG (2006) Carbon storage on landscapes with stand-replacing fires. Bioscience 56:598–606

Kasischke ES, Bruhwiler LP (2002) Emissions of carbon dioxide, carbon monoxide, and methane from boreal forest fires in 1998. J Geophys Res Atmos 108:8146

Kasischke ES, Christensen NL, Stocks BJ (1995) Fire, global warming, and the carbon balance of boreal forests. Ecol Appl 5:437–451

Khomik M, Arain MA, McCaughey JH (2006) Temporal and spatial variability of soil respiration in a boreal mixedwood forest. Agric For Meteorol 140:244–256

Krankina ON, Harmon ME (1995) Dynamics of the dead wood carbon pool in northwestern Russian boreal forests. Water Air Soil Poll 82:227–238

Krankina ON, Harmon ME, Griazkin AV (1999) Nutrient stores and dynamics of woody detritus in a boreal forest: modeling potential implications at the stand level. Can J For Res 29:20–32

Krause H (1998) Forest floor mass and nutrients in two chronosequences of plantations: jack pine vs. black spruce. Can J Soil Sci 78:77–83

Kurz WA, Apps MJ (1996) Retrospective assessment of carbon flows in Canadian boreal forests. In: Apps MJ, Price DT (eds) Forest ecosystems, forest management and the global carbon cycle, NATO ASI series 1: global environmental change. Springer, Heidelberg, pp 173–183

Laiho R, Prescott CE (2004) Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. Can J For Res 34:763–777

Lal R (2005) Forest soils and carbon sequestration. For Ecol Manag 220:242–258

Lamlom SH, Savidge RA (2003) A reassessment of carbon content in wood: variation within and between 41 North American species. Biomass Bioenerg 25:381–388

Lecomte N, Simard M, Fenton N, Bergeron Y (2006) Fire severity and long-term ecosystem biomass dynamics in coniferous boreal forests of eastern Canada. Ecosystems 9:1215–1230

Leduc SD, Rothstein DE (2007) Initial recovery of soil carbon and nitrogen pools and dynamics following disturbance in jack pine forests: a comparison of wildfire and clearcut harvesting. Soil Biol Biochem 39:2865–2876

Lee PC, Crites S, Nietfeld M, VanNguyen H, Stelfox JB (1997) Characteristics and origins of deadwood material in aspen-dominated boreal forests. Ecol Appl 7:691–701

Li Z, Kurz WA, Apps MJ, Beukema SJ (2003) Belowground biomass dynamics in the Carbon Budget Model of the Canadian Forest Sector: recent improvements and implications for the estimation of NPP and NEP. Can J For Res 33:126–136

Lindbladh M, Abrahamsson M, Seedre M, Jonsell M (2007) Saproxylic beetles in artificially created high-stumps of spruce

and birch within and outside hotspot areas. Biodivers Conserv 16:3213–3226
Litton CM, Raich JW, Ryan MG (2007) Carbon allocation in forest ecosystems. Glob Change Biol 13:2089–2109
Litton CM, Ryan MG, Tinker DB, Knight DH (2003) Belowground and aboveground biomass in young postfire lodgepole pine forests of contrasting tree density. Can J For Res 33:351–363
Longton RE (1992) The role of bryophytes and lichens in terrestrial ecosystems. In: Bates JW, Farmer AW (eds) Bryophytes and lichens in a changing environment. Clarendon Press, Oxford, pp 77–102
Luyssaert S, Schulze ED, Borner A, Knohl A, Hessenmoller D, Law BE, Ciais P, Grace J (2008) Old-growth forests as global carbon sinks. Nature 455:213–215
MacPherson DM, Lieffers VJ, Blenis PV (2001) Productivity of aspen stands with and without a spruce understory in Alberta's boreal mixedwood forests. For Chron 77:351–356
Magnani F, Mencuccini M, Borghetti M, Berbigier P, Berninger F, Delzon S, Grelle A, Hari P, Jarvis PG, Kolari P, Kowalski AS, Lankreijer H, Law BE, Lindroth A, Loustau D, Manca G, Moncrieff JB, Rayment M, Tedeschi V, Valentini R, Grace J (2007) The human footprint in the carbon cycle of temperate and boreal forests. Nature 447:848–850
Malhi Y, Baker TR, Phillips OL, Almeida S, Alvarez E, Arroyo L, Chave J, Czimczik CI, Di Fiore A, Higuchi N, Killeen TJ, Laurance SG, Laurance WF, Lewis SL, Montoya LMM, Monteagudo A, Neill DA, Vargas PN, Patino S, Pitman NCA, Quesada CA, Salomao R, Silva JNM, Lezama AT, Martinez RV, Terborgh J, Vinceti B, Lloyd J (2004) The above-ground coarse wood productivity of 104 neotropical forest plots. Glob Change Biol 10:563–591
Manies KL, Harden JW, Bond-Lamberty BP, O'Neill KP (2005) Woody debris along an upland chronosequence in boreal Manitoba and its impact on long-term carbon storage. Can J For Res 35:472–482
Marschner H (1995) Mineral nutrition of higher plants. Academic, London
Martin JL, Gower ST, Plaut J, Holmes B (2005) Carbon pools in a boreal mixedwood logging chronosequence. Glob Change Biol 11:1883–1894
Matamala R, Gonzàlez-Meler MA, Jastrow JD, Norby RJ, Schlesinger WH (2003) Impacts of fine root turnover on forest NPP and soil C sequestration potential. Science 302:1385–1387
McKechnie J, Colombo SJ, Chen J, Mabee W, MacLean HL (2011) Forest bioenergy or forest carbon? Assessing trade-offs in greenhouse gas mitigation with wood-based fuels. Environ Sci Technol (in press)
McRae DJ, Duchesne LC, Freedman B, Lynham TJ, Woodley S (2001) Comparisons between wildfire and forest harvesting and their implications in forest management. Environ Rev 9:223–260
Medlyn BE, Barton CVM, Broadmeadow MSJ, Ceulemans R, De Angelis P, Forstreuter M, Freeman M, Jackson SB, Kellomaki S, Laitat E, Rey A, Roberntz P, Sigurdsson BD, Strassemeyer J, Wang K, Curtis PS, Jarvis PG (2001) Stomatal conductance of forest species after long-term exposure to elevated CO_2 concentration: a synthesis. New Phytol 149:247–264
Medlyn BE, Berbigier P, Clement R, Grelle A, Loustau D, Linder S, Wingate L, Jarvis PG, Sigurdsson BD, McMurtrie RE (2005) Carbon balance of coniferous forests growing in contrasting climates: model-based analysis. Agric For Meteorol 131:97–124
Melillo JM, McGuire AD, Kicklighter DW, Moore B, Vorosmarty CJ, Schloss AL (1993) Global climate change and terrestrial net primary production. Nature 363:234–240
Micales JA, Skog KE (1997) The decomposition of forest products in landfills. Int Biodeterior Biodegr 39:145–158
Millard P, Sommerkorn M, Grelet GA (2007) Environmental change and carbon limitation in trees: a biochemical, ecophysiological and ecosystem appraisal. New Phytol 175:11–28
Mokany K, Raison RJ, Peokushkin AS (2006) Critical analysis of root: shoot ratios in terrestrial biomes. Glob Change Biol 12:84–96
Murty D, McMurtrie RE, Ryan MG (1996) Declining forest productivity in aging forest stands: a modeling analysis of alternative hypotheses. Tree Physiol 16:187–200
Nadelhoffer KJ, Raich JW (1992) Fine root production estimates and belowground carbon allocation in forest ecosystems. Ecology 73:1139–1147
Nalder IA, Wein RW (1999) Long-term forest floor carbon dynamics after fire in upland boreal forests of western Canada. Glob Biogeochem Cycle 13:951–968
Nalder IA, Wein RW (2006) A model for the investigation of long-term carbon dynamics in boreal forests of western Canada—I. Model development and validation. Ecol Model 192:37–66
Neff JC, Harden JW, Gleixner G (2005) Fire effects on soil organic matter content, composition, and nutrients in boreal interior Alaska. Can J For Res 35:2178–2187
Norby RJ, DeLucia EH, Gielen B, Calfapietra C, Giardina CP, King JS, Ledford J, McCarthy HR, Moore DJP, Ceulemans R, De Angelis P, Finzi AC, Karnosky DF, Kubiske ME, Lukac M, Pregitzer KS, Scarascia-Mugnozza GE, Schlesinger WH, Oren R (2005) Forest response to elevated CO_2 is conserved across a broad range of productivity. Proc Natl Acad Sci USA 102:18052–18056
O'Connell KEB, Gower ST, Norman JM (2003a) Comparison of NPP and light use dynamics of two boreal black spruce forest communities. Ecosystems 6:236–247
O'Connell KEB, Gower ST, Norman JM (2003b) Net ecosystem production of two contrasting boreal black spruce forest communities. Ecosystems 6:248–260
Ouimet R, Camire C, Brazeau M, Moore JD (2008) Estimation of coarse root biomass and nutrient content for sugar maple, jack pine, and black spruce using stem diameter at breast height. Can J For Res 38:92–100
Paré D, Bergeron Y (1995) Above-ground biomass accumulation along a 230-year chronosequence in the southern portion of the Canadian boreal forest. J Ecol 83:1001–1007
Pedlar JH, Pearce JL, Venier LA, McKenney DW (2002) Coarse woody debris in relation to disturbance and forest type in boreal Canada. For Ecol Manag 158:189–194
Peichl M, Arain AA (2006) Above- and belowground ecosystem biomass and carbon pools in an age-sequence of temperate pine plantation forests. Agric For Meteorol 140:51–63
Pienaar LV, Turnbull KJ (1973) The Chapman-Richards generalization of Von Bertalanffy's growth model for basal area growth and yield in even—aged stands. For Sci 19:2–22
Pregitzer KS, Euskirchen ES (2004) Carbon cycling and storage in world forests: biome patterns related to forest age. Glob Change Biol 10:2052–2077
Prescott CE, Maynard DG, Laiho R (2000) Humus in northern forests: friend or foe? For Ecol Manag 133:23–36
Preston CM, Trofymow JA, Niu J, Fyfe CA (1998) (13)CPMAS-NMR spectroscopy and chemical analysis of coarse woody debris in coastal forests of Vancouver Island. For Ecol Manag 111:51–68
Pumpanen J, Westman CJ, Ilvesniemi H (2004) Soil CO_2 efflux from a podzolic forest soil before and after forest clear-cutting and site preparation. Boreal Environ Res 9:199–212
Raison RJ, Woods PV, Jakobsen BF, Bary GAV (1986) Soil temperatures during and following low-intensity prescribed burning in a Eucalyptus-pauciflora forest. Aust J Soil Res 24:33–47

Rapalee G, Trumbore SE, Davidson EA, Harden JW, Veldhuis H (1998) Soil carbon stocks and their rates of accumulation and loss in a boreal forest landscape. Glob Biogeochem Cycle 12:687–701

Rothstein DE, Yermakov ZY, Buell AL (2004) Loss and recovery of ecosystem carbon pools following stand-replacing wildfire in Michigan jack pine forests. Can J For Res 34:1908–1918

Ruess RW, Hendrick RL, Vogel JG, Sveinbjornsson B (2006) The role of fine roots in the functioning of boreal forests. In: Chapin FS III, Oswood MW, Van Cleve K, Viereck L, Verbyla D (eds) Alaska's changing boreal forest. Oxford University Press, New York, pp 189–210

Ruess RW, Hendrick RL, Burton AJ, Pregitzer KS, Sveinbjornsson B, Allen ME, Maurer GE (2003) Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska. Ecol Monogr 73:643–662

Ruess RW, Vancleve K, Yarie J, Viereck LA (1996) Contributions of fine root production and turnover to the carbon and nitrogen cycling in taiga forests of the Alaskan interior. Can J For Res 26:1326–1336

Ryan MG, Binkley D, Fownes JH (1997) Age-related decline in forest productivity: pattern and process. Adv Ecol Res 27:213–262

Ryan MG, Binkley D, Fownes JH, Giardina CP, Senock RS (2004) An experimental test of the causes of forest growth decline with stand age. Ecol Monogr 74:393–414

Sandstrom F, Petersson H, Kruys N, Stahl G (2007) Biomass conversion factors (density and carbon concentration) by decay classes for dead wood of Pinus sylvestris, Picea abies and Betula spp. in boreal forests of Sweden. For Ecol Manag 243:19–27

Sathre R, O'Connor (2010) Meta-analysis of greenhouse gas displacement factors of wood product substitution. Environ Sci Policy 13:104–114

Schenk HJ, Jackson RB (2002) Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. J Ecol 90:480–494

Seedre M, Chen HYH (2010) Carbon dynamics of aboveground live vegetation of boreal mixedwoods after wildfire and clearcutting. Can J For Res 40:1862–1869

Senici D, Chen HYH, Bergeron Y, Cyr D (2010) Spatiotemporal variations of fire frequency in central boreal forest. Ecosystems 13:1227–1238

Shaver GR, Billings WD, Chapin FS, Giblin AE, Nadelhoffer KJ, Oechel WC, Rastetter EB (1992) Global change and the carbon balance of Arctic ecosystems. Bioscience 42:433–441

Shorohova EV, Shorohov AA (2001) Coarse woody debris dynamics and stores in a boreal virgin spruce forest. Ecol Bull 49:129–135

Shrestha BM, Chen HYH (2010) Effects of stand age, wildfire and clearcut harvesting on forest floor in boreal mixedwood forests. Plant Soil 336:267–277

Siitonen J, Martikainen P, Punttila P, Rauh J (2000) Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. For Ecol Manag 128:211–225

Siltanen RM, Apps MJ, Zoltai SC, Mair RM, Strong WL (1997) A soil profile and organic carbon data base for Canadian forest and tundra mineral soils. Nat Resour Can Can For Serv North For Cent Inf Rep Fo42-271/1997E

Simard DG, Fyles JW, Pare D, Nguyen T (2001) Impacts of clearcut harvesting and wildfire on soil nutrient status in the Quebec boreal forest. Can J Soil Sci 81:229–237

Sippola AL, Siitonen J, Kallio R (1998) Amount and quality of coarse woody debris in natural and managed coniferous forests near the timberline in Finnish Lapland. Scand J For Res 13:204–214

Smith CK, Coyea MR, Munson AD (2000) Soil carbon, nitrogen, and phosphorus stocks and dynamics under disturbed black spruce forests. Ecol Appl 10:775–788

Smith FW, Long JN (2001) Age-related decline in forest growth: an emergent property. For Ecol Manag 144:175–181

Spiecker H, Mielikainen K, Kohl M, Skovsgaars J (1996) Growth trends in European forest—studies from 12 countries. Springer, Berlin

Spiecker H (1999) Overview of recent growth trends in European forests. Water Air Soil Poll 116:33–46

Spies TA, Franklin JF, Thomas TB (1988) Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology 69:1689–1702

Steele SJ, Gower ST, Vogel CS, Norman JM (1997) Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. Tree Physiol 17:577–587

Strand AE, Pritchard SG, McCormack ML, Davis MA, Oren R (2008) Irreconcilable differences: fine-root life spans and soil carbon persistence. Science 319:456–458

Sturtevant BR, Bissonette JA, Long JN, Roberts DW (1997) Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. Ecol Appl 7:702–712

Taylor AR, Wang JR, Kurz WA (2008) Effects of harvesting intensity on carbon stocks in eastern Canadian red spruce (*Picea rubens*) forests: an exploratory analysis using the CBM-CFS3 simulation model. For Ecol Manag 255:3632–3641

Ter-Mikaelian MT, Colombo SJ, Chen J (2008) Amount of downed woody debris and its prediction using stand characteristics in boreal and mixedwood forests of Ontario, Canada. Can J For Res 38:2189–2197

Thomas KD, Prescott CE (2000) Nitrogen availability in forest floors of three tree species on the same site: the role of litter quality. Can J For Res 30:1698–1706

Tinker DB, Knight DH (2001) Temporal and spatial dynamics of coarse woody debris in harvested and unharvested lodgepole pine forests. Ecol Model 141:125–149

Trofymow JA, Moore TR, Titus B, Prescott C, Morrison I, Siltanen M, Smith S, Fyles J, Wein R, CamirT C, Duschene L, Kozak L, Kranabetter M, Visser S (2002) Rates of litter decomposition over 6 years in Canadian forests: influence of litter quality and climate. Can J For Res 32:789–804

Trumbore S (2000) Age of soil organic matter and soil respiration: radiocarbon constraints on belowground C dynamics. Ecol Appl 10:399–411

Trumbore SE, Gaudinski JB (2003) The secret lives of roots. Science 302:1344–1345

Van Oijen M, Cannell MGR, Levy PE (2004) Modelling biogeochemical cycles in forests: state of the art and perspectives. In: Andersson F, Birot Y, Päivinen R (eds) Towards the sustainable use of Europe's forests—forest ecosystem and landscape research: scientific challenges and opportunities 49:157–169

Vogt KA, Vogt DJ, Bloomfield J (1998) Analysis of some direct and indirect methods for estimating root biomass and production of forests at an ecosystem level. Plant Soil 200:71–89

Vogt KA, Vogt DJ, Palmiotto PA, Boon P, Ohara J, Asbjornsen H (1996) Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant Soil 187:159–219

Wang CK, Bond-Lamberty B, Gower ST (2002) Environmental controls on carbon dioxide flux from black spruce coarse woody debris. Oecologia 132:374–381

Wang CK, Bond-Lamberty B, Gower ST (2003) Carbon distribution of a well- and poorly-drained black spruce fire chronosequence. Glob Change Biol 9:1066–1079

Wardle DA, Walker LR, Bardgett RD (2004) ecosystem properties and forest decline in contrasting long-term chronosequences. Science 305:509–513

Weber MG, Flannigan MD (1997) Canadian boreal forest ecosystem structure and function in a changing climate: impact on fire regimes. Environ Rev 5:145–166

Weedon JT, Cornwell WK, Cornelissen JHC, Xanne AE, Wirth C, Coomes DA (2009) Global meta-analysis of wood decomposition rates: a role for trait variation among tree species? Ecol Lett 12:45–56

Xing ZS, Bourque CPA, Swift DE, Clowater CW, Krasowski M, Meng FR (2005) Carbon and biomass partitioning in balsam fir (Abies balsamea). Tree Physiol 25:1207–1217

Yanai RD, Currie WS, Goodale CL (2003a) Soil carbon dynamics after forest harvest: an ecosystem paradigm reconsidered. Ecosystems 6:197–212

Yanai RD, Park BB, Hamburg SP (2006) The vertical and horizontal distribution of roots in northern hardwood stands of varying age. Can J For Res 36:450–459

Yanai RD, Stehman SV, Arthur MA, Prescott CE, Friedland AJ, Siccama TG, Binkley D (2003b) Detecting change in forest floor carbon. Soil Sci Soc Am J 67:1583–1593

Yatskov M, Harmon ME, Krankina ON (2003) A chronosequence of wood decomposition in the boreal forests of Russia. Can J For Res 33:1211–1226

Yermakov Z, Rothstein DE (2006) Changes in soil carbon and nitrogen cycling along a 72-year wildfire chronosequence in Michigan jack pine forests. Oecologia 149:690–700

Yuan ZY, Chen HYH (2010) Fine root biomass, production, turnover rates, and nutrient contents in boreal forest ecosystems in relation to species, climate, fertility, and stand age: literature review and meta-analyses. Crit Rev Plant Sci 29:204–221

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CARBON DYNAMICS OF ABOVEGROUND LIVE VEGETATION OF BOREAL MIXEDWOODS AFTER WILDFIRE AND CLEARCUTTING.

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NOTE / NOTE

Carbon dynamics of aboveground live vegetation of boreal mixedwoods after wildfire and clear-cutting

Meelis Seedre and Han Y.H. Chen

Abstract: Live vegetation carbon (C) pool dynamics are central to understanding C sequestration of forest ecosystems. Despite its importance, how aboveground live C pools change with stand development in boreal mixedwoods is poorly understood. We quantified aboveground live C pools (i.e., trees, >4 m in height; saplings and shrubs, 1.3–4 m in height; and understory plants, <1.3 m in height) in a postfire chronosequence ranging from 1 to 203 years and a postlogging chronosequence ranging from 1 to 27 years in the boreal mixedwoods of central Canada. The tree C pool of postfire stands increased from 0 to 109.2 Mg/ha from 1 to 92 years after fire and then declined to approximately 70 Mg/ha in 140- and 203-year-old stands. Carbon pools of saplings and shrubs and understory plants also changed with stand development and stand origin. Of the three age classes compared, postlogged stands had significantly higher vegetation C than postfire stands 1 and 27 years after disturbance, but there was no difference in 9-year-old stands. Higher values of live vegetation C in postlogged stands was attributed to live standing trees left after logging and silvicultural treatments that helped trees to establish during stand initiation.

Résumé : La dynamique des réservoirs de carbone (C) que constitue la végétation vivante est primordiale pour comprendre la séquestration de C dans les écosystèmes forestiers. Malgré son importance, la façon dont les réservoirs de C constitués de la partie aérienne de la végétation vivante changent en fonction du développement des peuplements dans les forêts boréales mixtes est mal comprise. Nous avons quantifié les réservoirs de C constitués de la partie aérienne de la végétation vivante, c.-à-d. les arbres (hauteur > 4 m), les gaules et les arbustes (hauteur de 1,3 à 4 m) et les plantes de sous-bois (hauteur < 1,3 m) pour une chronoséquence issue de feux allant de 1 à 203 ans et pour une chronoséquence issue de coupes allant de 1 à 27 ans dans les forêts boréales mixtes du centre du Canada. Le réservoir de C dans les arbres des peuplements issus de feux augmentait de 0 à 109,2 Mg/ha de 1 à 92 ans après un feu et diminuait par la suite à environ 70 Mg/ha dans les peuplements âgés de 140 à 203 ans. Les réservoirs de C dans les gaules, les arbustes et la végétation du sous-bois ont aussi changés selon le développement et l'origine du peuplement. Parmi les trois classes d'âge qui ont été comparées, il y avait significativement plus de C dans la végétation des peuplements issus de coupes que dans les peuplements issus de feux 1 et 27 ans après la perturbation mais il n'y avait pas de différence dans les peuplements âgés de neuf ans. Les valeurs plus élevées de C dans la végétation vivante des peuplements issus de coupes ont été attribuées aux arbres vivants laissés debout après la coupe et aux traitements sylvicoles qui ont favorisé l'établissement des arbres pendant l'initiation du peuplement.

[Traduit par la Rédaction]

Introduction

Carbon (C) dynamics of northern forests are largely driven by disturbances and subsequent stand development (Pregitzer and Euskirchen 2004; Bond-Lamberty et al. 2007; Magnani et al. 2007; Luyssaert et al. 2008). Among all C pools in boreal forests, live vegetation C accounts for a major component of total C accumulation and is most dynamic through stand development in boreal forests (Taylor et al. 2007, 2008; Bernier et al. 2010). Live vegetation C yield after wildfire in single-species stands has been shown to follow a sigmoidal pattern (Gower et al. 2001; Wang et al. 2003; Taylor et al. 2007), i.e., vegetation C initially increases rapidly and, after reaching its maximum, remains unchanged. However, few studies have examined C dynamics of boreal mixedwoods, despite it being the most productive and diverse boreal ecosystem in North America (Chen and Popadiouk 2002) and covering approximately 25%–50% of the boreal forest (Steyaert et al. 1997). A postfire

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chronosequence (27–230 years since fire) of boreal mixedwoods (Paré and Bergeron 1995) indicates that, similar to single-species stands, long-term biomass accumulation initially increases rapidly with stand age but declines through succession. This phenomenon is attributed to the diminishing role of trembling aspen (*Populus tremuloides* Michx.), which is the most productive species in boreal forest, and to the effect of spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks at the late stages of stand development.

Beside forest fires that affect several million hectares of Canada's boreal forest, timber harvesting (mostly mechanical clear-cutting) has been an important stand replacing disturbance at a rate of approximately 900 000 ha/year (Canadian Coucil of Forest Ministers 2005). Carbon dynamics may differ significantly with disturbance origin (Pregitzer and Euskirchen 2004; Brassard and Chen 2006). The effect of clear-cutting on postdisturbance vegetation C accumulation may be different from that of fire (Pinard and Cropper 2000; Ruel et al. 2004; Gough et al. 2007). In the boreal forest, several chronosequence studies of aboveground biomass have shown large differences in various C pools between young postlogged stands and older postfire stands (e.g., Fleming and Freedman 1998; Howard et al. 2004; Fredeen et al. 2005; Martin et al. 2005; Taylor et al. 2007). However, it is unclear how stands of similar ages differ in C pools between fire and logging origins.

This study attempted to (*i*) quantify the changes in aboveground live vegetation C pools in a postfire chronosequence of boreal mixedwoods and (*ii*) compare aboveground live vegetation C dynamics of mixedwood stands after wildfire and clear-cutting. We hypothesized that total tree C would decline after reaching maximum biomass because of species replacement from more productive pioneer tree species to late-successional species during succession. We also hypothesized that postlogged sites would have more live tree aboveground C compared with postfire sites because of the presence of advanced regeneration after clear-cutting and subsequent silvicultural treatments that foster establishment and growth of trees. In this study, we sampled postfire stands with six age classes ranging from 1 to 203 years since fire; however, postlogged stands were sampled only for 1, 9, and 27 years after clear-cutting because large-scale commercial logging only took place approximately three decades ago in the study area. Thus, comparison for stand origins was made for only younger stands, similar to the studies of dynamics of live tree structural diversity (Brassard et al. 2008), coarse woody debris (Brassard and Chen 2008), and understory vegetation (Hart and Chen 2008).

Materials and methods

Study area

The study was conducted in the boreal mixedwood forest region located approximately 150 km north of Thunder Bay, Ontario, from 49°27′N to 49°38′N and from 89°29′W to 89°54′W. The study area belongs to the Lake Nipigon ecoregion and Moist Mid-Boreal ecoclimatic region (Ecological Stratification Working Group 1996). This ecoregion, which surrounds Lake Nipigon and extends westward from the north shore of Lake Superior to Lake St. Joseph in northwestern Ontario, is characterized by warm summers and cold, snowy winters. Mean annual temperature of 2.5 °C and mean annual precipitation of 712 mm (559 mm rain and 188 mm snow) are recorded at the closest meteorological station to study area, Thunder Bay, Ontario (48°22′N, 89°19′W, 199 m elevation) (Environment Canada 2008). The length of the growing season is approximately 160 days with a mean growing season temperature of 12.3 °C (Environment Canada 2008). Topographic features in this area were shaped by the retreat of the Laurentide Ice Sheet approximately 10 000 years ago. Soil type on upland sites is relatively deep glacial till of the Brunisolic order (Soil Classification Working Group 1996).

Stand-replacing crown fire is the main natural stand initiating disturbance in the area. Mean fire return interval of the region is unknown but is likely intermediate to the shorter fire cycles of the western boreal forest (75 years) and longer fire cycles of the eastern boreal forest (100 years) (Bergeron 1991; Weir et al. 2000). The dominant tree species in the study area are jack pine (*Pinus banksiana* Lamb.), *Populus tremuloides*, paper birch (*Betula papyrifera* Marsh.), black spruce (*Picea mariana* (Mill.) BSP), white spruce (*Picea glauca* (Moench) Voss), and balsam fir (*Abies balsamea* (L.) Mill.), and these occur in mixed dominance. Detailed information on understory vegetation abundance, diversity, and composition can be found in Hart and Chen (2008).

Changes in tree species composition occur during stand development in boreal forests (Chen and Popadiouk 2002). Although multiple successional pathways can occur depending on site characteristics, surrounding stands, and minor disturbances, shifts in canopy dominance from shade-intolerant species to mixed coniferous–deciduous or coniferous species in postfire stands are the predominant pathways in the central boreal mixedwood region (Brassard and Chen 2008; Brassard et al. 2008; Taylor and Chen 2010). In this study, we sampled stands dominated by *Populus tremuloides* and *Pinus banksiana* at early stages and stands dominated by *Picea mariana*, *A. balsamea*, and *B. papyrifera* at later stages of stand development (Table 1). To limit the effect of site condition on aboveground live biomass accumulation, we deliberately selected mesic sites on flat midslope positions (with no slope >5%) on well-drained glacial moraines (>50 cm in thickness). All stands selected were at least 1 ha in area and were visually homogeneous in structure and composition. A soil pit was dug in each sampled stand to verify whether site was mesic following the procedure described in Taylor et al. (2000).

Data collection

Because of the difficulty in choosing a well-balanced design to study the effects of disturbances (Turner et al. 1997; Parker and Wiens 2005), we used post facto designs recommended by Parker and Wiens (2005). Every effort was made to intersperse sample stands to minimize the effect of spatial structure (Legendre and Legendre 1998). Interspersion was achieved by selecting stands of the same age and disturbance origin from different road accesses, which resulted in several kilometres between selected stands. However, a complete interspersion of sampled stands was impossible because of fire history and fire size in the study area. For in-

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Table 1. Stand characteristics (mean and standard error of the mean) of 27 stands sampled in northwestern Ontario.

Origin and TSD (years)	Stand density (stems/ha) or basal area (m^2/ha)†	Stand composition (%)*					
		Abies balsamea	*Betula papyrifera*	*Picea glauca*	*Picea mariana*	*Pinus banksiana*	*Populus tremuloides*
Fire							
1	0	0	0	0	0	0	0
9	21 917 ± 3619	3	9	0	2	26	60
27	7.06 ± 0.6	0	1	0	12	61	26
92	45.30 ± 6.0	4	3	4	20	28	40
140	31.56 ± 7.5	29	2	0	35	8	26
203	31.28 ± 2.4	21	42	31	5	0	1
Logging							
1	833 ± 83	0	0	0	0	27	73
9	21 050 ± 2344	0	27	0	10	22	41
27	27.95 ± 1.5	2	22	2	9	36	30

Note: Each stand age class and stand origin was replicated three times. TSD, time since disturbance.

*Stand composition was determined based on stand density for 1- and 9-year-old stands and on basal area for older stands.

†Stand density was determined for 1- and 9-year-old stands, and stand basal area was determined for older stands. Values are means ± SEs.

stance, we found only one 27-year-old fire of approximately 120 000 ha in size.

Field work took place in summer 2007. To study the effects of time since disturbance (TSD), stands of fire origin were selected to represent all developmental phases of mixedwood succession: stand initiation (1- and 9-year-old stands), stem exclusion (27-year-old stands), canopy transition (92- and 140-year-old stands), and gap dynamics (203-year-old stands) stages (Chen and Popadiouk 2002). Based on the fire history of the area, six TSD classes were chosen for the postfire chronosequence with stand age ranging from 1 to 203 years (Table 1). Postfire sites regenerated naturally without any subsequent anthropogenic disturbances.

Large-scale commercial logging began in the early 1970s in the study area. We sampled previously logged stands of ages 1, 9, and 27 years. All postlogged stands were clear-cut harvested but differed somewhat in the logging method. In 1- and 9-year-old stands, trees were felled and dragged to roadside for processing. In 27-year-old stands, trees were felled, topped, and delimbed at the stump before being dragged to roadside. After logging, all postlogged sites were artificially regenerated (aerial seeding with *Pinus banksiana*) to achieve desirable species composition. Each stand origin and stand age class was replicated three times, resulting in 27 sampled stands.

The TSD was determined for each stand sampled. For stands <70 years old, time since last stand-replacing disturbance was determined by using detailed fire and harvesting records. For older postfire stands, time since fire had been previously determined using cores at breast height or disks cut at the base from postfire *Pinus banksiana* trees (see Brassard and Chen 2008). The cores and disks were brought to the laboratory. In the laboratory, the cores were mounted on constructed core strips, and disks were cut transversely and sanded to make rings visible. Rings were then counted using a hand-held magnifier until the same count was obtained three successive times. If cores were taken from breast height (1.3 m above the ground), tree ages were corrected to time since fire by adding 7 years using the model developed by Vasiliauskas and Chen (2002). For the oldest burned area, one live *Pinus banksiana* tree and seven *Pinus banksiana* snags were sampled and disks were cut at the base of stems. The age of the live tree was 203 years, and the ages of the snags ranged from 140 to 180 years. We used the live tree age as the time since fire for the area.

Within each sampled stand, a 400 m^2 circular plot was established within which diameters at breast height (DBHs; 1.3 m above the root collar) were measured for all overstory trees (DBH ≥10 cm). Heights of at least three randomly chosen trees of each species per plot were measured using a TruPulse™ 200 laser rangefinder. To estimate the heights of remaining trees, a height–diameter curve was developed for each tree species by pooling height–diameter measurements from all sampled stands (see Brassard et al. 2008). For understory trees (DBH <10 cm, but height >4 m), heights and DBHs were measured in a 100 m^2 plot located within the 400 m^2 plot. Heights and DBHs of tree saplings and tall shrubs (1.3–4 m in height) were measured in ten 2 m × 2 m subplots randomly located within the 400 m^2 plot. Stand characteristics were summarized based on tree measurements (see Table 1). For stands older than 27 years, stand basal area was reported. Because of the small sizes of trees in the 1- and 9-year-old stands, tree density (stems/ha) was used to quantify stand composition.

Understory vascular plant biomass (trees and shrubs <1.3 m in height and herbaceous plants) was estimated by harvesting ten 1 m × 1 m subplots located within the 400 m^2 circular plot. Plants were clipped at the base, stored in airtight bags, and transported daily to the laboratory for determination of biomass. Samples were oven-dried at 70 °C for 48–72 h and weighed. Bryophyte biomass was estimated by harvesting five 25 cm × 25 cm subplots located within the 400 m^2 circular plot. After conversion to biomass per hectare, understory vascular plants and bryophytes were pooled as understory plants in subsequent analyses.

Aboveground live biomass (the sum of stem, branch, and foliage biomass) was estimated from height and DBH for

Table 2. The effects of time since disturbance (TSD) and stand origin on C pools of trees, saplings and shrubs, understory vascular plants, and bryophytes.

Carbon pool and source of variation	df	MS	*F*	*P*	η^2 (%)
Trees					
TSD	5	57.55	55.45	**<0.001**	84
Origin	1	23.35	22.503	**<0.001**	7
TSD × origin	2	6.00	5.78	**0.012**	4
Error	18	1.04			
Saplings and shrubs					
TSD	5	3.77	7.16	**0.001**	54
Origin	1	3.55	6.74	**0.018**	10
TSD × origin	2	1.62	3.08	0.071	9
Error	18	0.53			
Understory plants					
TSD	5	0.46	3.41	**0.024**	49
Origin	1	0.15	1.09	0.311	6
TSD × origin	2	0.91	6.76	**0.006**	43
Error	18	0.13			
Total live C					
TSD	5	50.53	50.37	**<0.001**	85
Origin	1	18.94	18.88	**<0.001**	6
TSD × origin	2	4.44	4.43	**0.027**	3
Error	18	1.00			

trees using allometric equations from Lambert et al. (2005) and for saplings and shrubs from Smith and Brand (1983). The biomass of tree components was converted to C based on the estimation that C content is 50% of oven-dry wood tissue and 45% of foliage tissue (Bisbee et al. 2001; Intergovernmental Panel on Climate Change 2003). Carbon content for plants other than trees was assumed to be 45% of dry biomass (Bisbee et al. 2001; Intergovernmental Panel on Climate Change 2003).

Data analysis

With exception of sapling and shrub C, data were not normally distributed according to a Shapiro–Wilk test, and the variances were also not homogeneous according to Levene's statistic. To meet these assumptions, square root transformations were applied.

The following general linear model was used to test the effect of time since disturbance (T; i = 1, 2, …, 6) and stand origin (O; j = 1, 2):

$$[1] \qquad Y_{ijk} = \mu + T_i + O_j + T \times O_{ij} + \varepsilon_{(ij)k}$$

where Y_{ijk} is C content of live trees, saplings and shrubs, understory plants, or total live vegetation. The TSD was treated as a categorical variable. Because of the unbalanced study design (i.e., missing cells), a type IV sum of squares was used (Shaw and Mitchellolds 1993). To estimate the proportion of total variance explained by an effect, we calculated η^2 (%) values (Pierce et al. 2004). Least squares of the differences post hoc tests were performed to determine differences (α = 0.05) among means. Statistical analyses were conducted using SPSS version 11 software (SPSS Inc. 2001).

Results

Live tree C

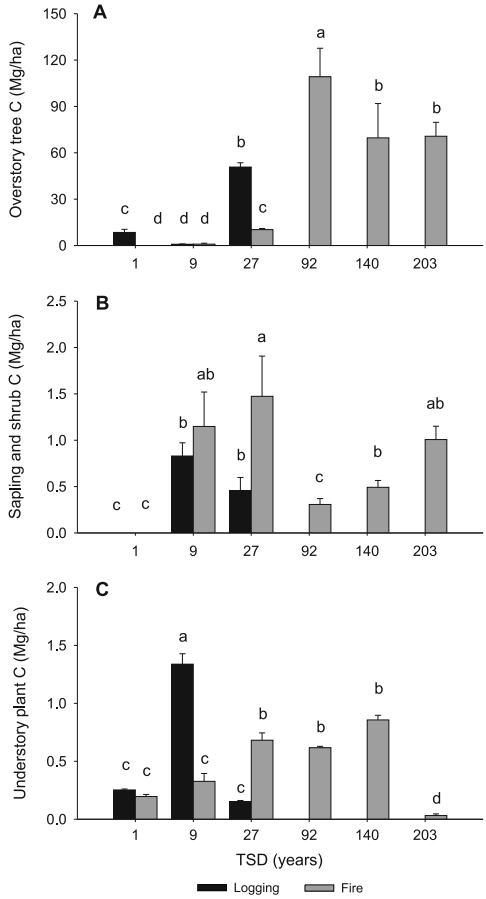
The TSD, stand origin and their interactions significantly influenced C pool of trees (Table 2, Fig. 1). Tree C pool increased from 0 Mg/ha immediately after fire to 0.8 Mg/ha in 9-year-old stands, 10.3 Mg/ha in the 27-year-old stand, 109.2 Mg/ha in the 92-year-old stand, and then declined to approximately 70 Mg/ha in both 140- and 203-year-old stands (Fig. 1).

Logging-origin stands had more live tree C than fire-origin stands in 1- and 27-year-old stands but not in 9-year-old stands (Table 2, Fig. 1). Live tree C pool was 8.4 Mg/ha in 1-year-old postlogged stands (0 Mg/ha in 1-year-old postfire stands) and 40.5 Mg/ha greater in 27-year-old postlogged than in postfire stands, whereas the C pool was approximately 0.8 Mg/ha in 9-year-old stands of both origins.

Sapling and shrub C

The sapling and shrub C pool also differed significantly with TSD and stand origin: TSD explained 54% of the variation (Table 2). In postfire stands, the pool increased from 0 Mg/ha in 1-year-old stands, to 1.7 Mg/ha in 9-year-old stands, and to 3 Mg/ha in 27 year-old stands; the pool decreased in 92- and 140-year-old stands and then increased to approximately 2 Mg/ha in 203-year-old stands (Fig. 1). Compared with postfire stands of the same age, the C pool was smaller in 9- and 27-year-old postlogged stands (Fig. 1). Sapling and shrub C pool accounted for a small percentage of live vegetation C in all ages except 9-year-old stands (Fig. 2). In 9-year-old stands, the C pool constituted 44% and 66% of total live aboveground C in postlogged and postfire stands, respectively (Fig. 2). The pool's

Fig. 1. Aboveground live carbon pools in relation to time since disturbance (TSD, years) and stand origin (fire and logging) for (A) trees (>4 m in height), (B) saplings and shrubs (1.3–4 m in height), and (C) understory plants (<1.3 m in height). Error bars are SEs. Bars with the same letter are not significantly different ($P < 0.05$).

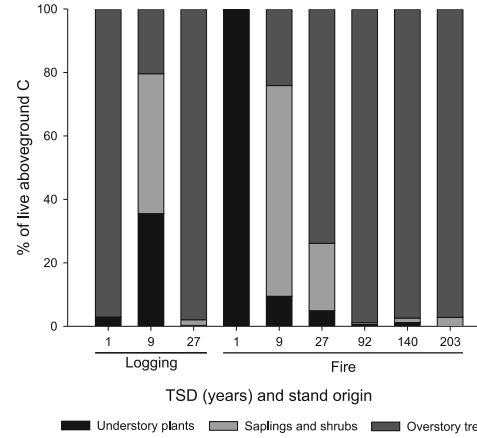


contribution was 22% in 27-year-old postfire sites (3 Mg/ha), which was the highest among all sites. Their share was <3% of total live vegetation C in all other cases.

Understory plant C

The C pool of understory plants also differed significantly with TSD and stand origin (Table 2, Fig. 1). In postfire stands, the C pool increased from 0.2 Mg/ha in 1-year-old stands to approximately 1 Mg/ha in 140-year-old stands but decreased greatly in 203-year-old stands, which coincided with higher sapling and shrub C at this stage (Fig. 1). Compared with postfire stands, the understory C pool in post-

Fig. 2. Percentages of total aboveground live carbon in trees (>4 m in height), saplings and shrubs (1.3–4 m in height), and understory plants (<1.3 m in height). TSD, time since disturbance.



logged stands was significantly higher in 9-year-old stands but lower in 27-year-old stands, whereas there was no difference between the two stand origins in 1-year-old stands. Understory plants were the only living plants in 1-year-old postfire stands; they constituted 35% and 9.5% of the live aboveground C 9 years after logging and fire, respectively, whereas their contribution was much smaller in other age classes (Fig. 2).

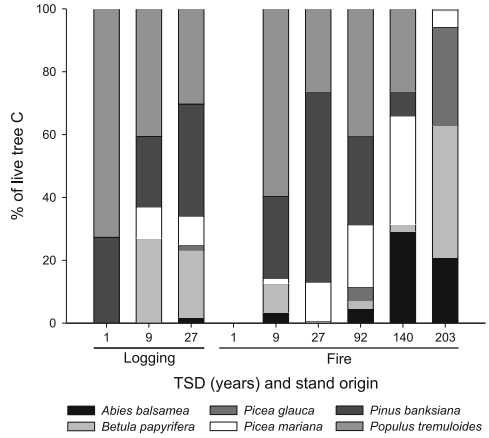
The C pool of all live vegetation followed a pattern similar that of only the trees; this pool constituted the largest share of live vegetation C (Fig. 2). The total C pool was significantly affected by TSD, stand origin, and the TSD × stand origin interaction (Table 2). In postfire stands, total live vegetation C pools were 0.2, 3.5, 13.9, 110.4, 71.5, and 72.7 Mg/ha at 1, 9, 27, 92, 140, and 203 years since fire. In postlogged stands, total live vegetation C pools were 8.7, 3.8, and 51.8 Mg/ha for 1-, 9-, and 27-year-old stands, respectively.

Discussion

Our results support the hypothesis that, after fire, long-term live vegetation biomass or C initially increases rapidly, reaches the maximum stand C, and then declines with increasing stand age. The rapid increase is consistent with several previous studies in which no canopy succession was observed (Wang et al. 2003; Martin et al. 2005; Taylor et al. 2007). The decline in the late stages of stand development was accompanied by a successional change from productive pioneer tree species to late-successional species (Table 1). The growth dynamics seen in this study are similar to the general pattern of biomass accumulation described by Sprugel (1985) and those observed in eastern (Paré and Bergeron 1995) and central (Brassard et al. 2008) boreal mixedwoods.

Although the decline in growth and C accumulation is common in many forest ecosystems (Ryan et al. 1997), the

Fig. 3. Percentages of total carbon in live trees (>4 m in height) by species in relation to stand origin and time since disturbance (TSD, years).



underlying causes are still unclear. Nutrient limitation and decreased photosynthetic capacity (Gower et al. 1996; Ryan et al. 1997) are often thought to result in growth and biomass declines. Ryan et al. (2004) studied tropical forests and found that neither nutrient limitation nor photosynthetic capacity was responsible for the decline, but the decline of aboveground production with stand age was a result of increased allocations of primary production to belowground biomass and foliage respiration.

Although biomass allocation and nutrient limitations in northern forest ecosystems may also be responsible for biomass decline, successional changes in species composition (Bormann and Sidle 1990) and increased probabilities of insect and (or) wind damage (Paré and Bergeron 1995; Chen and Popadiouk 2002) also likely contribute. In our stands, *Populus tremuloides* abundance declined from 40% of the total stand C in 92-year-old stands, to 26% in 140-year-old stands, and to only 1% in 203-year-old stands (Fig. 3). The decreasing share of *Populus tremuloides* is known to have a significant negative influence on stand biomass (Paré and Bergeron 1995). The decline in stand biomass reported by Paré and Bergeron (1995) was also attributed to spruce budworm outbreaks. Our stands also experienced some spruce budworm outbreaks (P. Poschmann, Abitibi-Bowater, Thunder Bay, Ont., personal communication, 2009) but, likely, to a lesser extent than those stands Paré and Bergeron (1995) studied because the spruce budworm outbreaks tend to be more severe in eastern than central boreal mixedwoods (Chen and Popadiouk 2002).

Although tree C accounted for the majority of total aboveground C in older stands, understory vegetation C was a significant component in early stages of stand development. Stand-replacing wildfire consumes most of forest floor and vegetation, which results in low understory C immediately after disturbance; however, resources and suitable growing spaces become available to allow plants to rapidly colonize the site. In contrast to the findings that understory vegetation abundance (measured as percent cover) is often higher in younger stands (De Grandpré et al. 1993; Hart and Chen 2006; Hart and Chen 2008), our results indicated an overall increasing trend of total understory C pool through stand development but a decline in the 203-year-old stands. The difference between patterns of cover and C or biomass pool is most likely attributed to understory plants in older stands being taller and having higher proportions of their biomass in stems and branches than in leaves, which greatly affects cover estimates. The decline observed in the 203-year-old stands seems to be a result of increased competition from the sapling and shrub layer, mostly beaked hazel (*Corylus cornuta* Marsh.) and green alder (*Alnus viridis* (Chaix.) DC.), which was significantly thicker in the oldest stands than in the younger stands (M. Seedre and H.Y.H. Chen, personal observation).

Aboveground tree C was different following wildfire and clear-cutting (Table 2). Postlogged stands generally had more aboveground live C than postfire stands. The difference found in stands 1 year after disturbance was attributed to residual live trees left after logging that were not present after wildfire in our sampled stands. However, such a difference may not occur when postfire stands have live trees standing after the fire. There was no difference between postfire and postlogged stands 9 years after disturbance, but there was significantly more biomass C 27 years after logging than fire (Fig. 1). This large difference is attributed to silvicultural treatments in the managed stands that allowed rapid stand establishment and fast capture of site resources by trees. The difference in species composition may also account for the difference in biomass C between postfire and postlogged stands at 27 years after disturbance (Table 1). At this age, the postfire stands had a greater *Pinus banksiana* component and less *B. papyrifera* (Fig. 3). Because hardwoods have higher productivity (Gower et al. 1997), the presence of *B. papyrifera* increased the C pool in postlogged stands.

The difference in understory plant C between postfire and postlogged stands seems to be a result of overstory competition and the size definitions of vegetation layers. For 27-year-old stands, the significantly smaller C pools of saplings and shrubs and understory plants in postlogged stands is likely attributable to the fact that most site resources were consumed by the more productive overstory. In the 9-year-old stands, there was no difference in total aboveground C between the two stand origins. On the same site condition, height growth of *Populus tremuloides* is greater than that of *B. papyrifera* (Vasiliauskas and Chen 2002). The greater amount of understory plant C and smaller amount of sapling and shrub C in these postlogged stands are attributed to a greater proportion of slower growing *B. papyrifera* that was classified as understory plants (i.e., <1.3 m in height), whereas a higher proportion of fast-growing *Populus tremuloides* in postfire stands resulted in a greater amount of sapling and shrub C.

Our results showed that logged mixedwood stands growing in similar soil and climatic conditions can have significantly greater aboveground live vegetation C compared with postfire stands of the same age. Because aboveground live vegetation C accumulation accounts for the major com-

ponent of ecosystem C sequestration and is highly associated with leaf litterfall and belowground root production (Wang et al. 2002; Chen and Klinka 2003; Bernier et al. 2010), our findings suggest that managed forest stands have higher C sequestration rates than unmanaged stands at comparable ages up to at least 27 years in the boreal mixedwood forests of central Canada.

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References

Bergeron, Y. 1991. The influence of island and mainland lakeshore landscapes on boreal forest fire regimes. Ecology, **72**(6): 1980–1992. doi:10.2307/1941553.

Bernier, P.Y., Guindon, L., Kurz, W.A., and Stinson, G. 2010. Reconstructing and modelling 71 years of forest growth in a Canadian boreal landscape: a test of the CBM-CFS3 carbon accounting model. Can. J. For. Res. **40**(1): 109–118. doi:10.1139/X09-177.

Bisbee, K.E., Gower, S.T., Norman, J.M., and Nordheim, E.V. 2001. Environmental controls on ground cover species composition and productivity in a boreal black spruce forest. Oecologia (Berl.), **129**(2): 261–270. doi:10.1007/s004420100719.

Bond-Lamberty, B., Peckham, S.D., Ahl, D.E., and Gower, S.T. 2007. Fire as the dominant driver of central Canadian boreal forest carbon balance. Nature (Lond.), **450**(7166): 89–92. doi:10.1038/nature06272. PMID:17972883.

Bormann, B.T., and Sidle, R.C. 1990. Changes in productivity and distribution of nutrients in a chronosequence at Glacier Bay National Park, Alaska. J. Ecol. **78**(3): 561–578. doi:10.2307/2260884.

Brassard, B.W., and Chen, H.Y.H. 2006. Stand structural dynamics of North American boreal forests. Crit. Rev. Plant Sci. **25**(2): 115–137. doi:10.1080/07352680500348857.

Brassard, B.W., and Chen, H.Y.H. 2008. Effects of forest type and disturbance on diversity of coarse woody debris in boreal forest. Ecosystems, **11**(7): 1078–1090. doi:10.1007/s10021-008-9180-x.

Brassard, B.W., Chen, H.Y.H., Wang, J.R., and Duinker, P.N. 2008. Effects of time since stand-replacing fire and overstory composition on live-tree structural diversity in the boreal forest of central Canada. Can. J. For. Res. **38**(1): 52–62. doi:10.1139/X07-125.

Canadian Coucil of Forest Ministers. 2005. Criteria and indicators of sustainable forest management in Canada: national status 2005. Natural Resouces Canada, Canadian Forest Service, Ottawa, Ont.

Chen, H.Y.H., and Klinka, K. 2003. Aboveground productivity of western hemlock and western redcedar mixed-species stands in southern coastal British Columbia. For. Ecol. Manage. **184**(1–3): 55–64. doi:10.1016/S0378-1127(03)00148-8.

Chen, H.Y.H., and Popadiouk, R.V. 2002. Dynamics of North American boreal mixedwoods. Environ. Rev. **10**(3): 137–166. doi:10.1139/a02-007.

De Grandpré, L., Gagnon, D., and Bergeron, Y. 1993. Changes in the understory of Canadian southern boreal forest after fire. J. Veg. Sci. **4**(6): 803–810. doi:10.2307/3235618.

Ecological Stratification Working Group. 1996. A national ecological framework for Canada. Agriculture and Agri-Food Canada, Research Branch, Centre for Land and Biological Resources Research, and Environment Canada, State of the Environment Directorate, Ecozone Analysis Branch, Ottawa, Ont.

Environment Canada. 2008. Climate normals for Thunder Bay, ON, Canada (1971–2000) [online]. Environment Canada, Meteorological Service of Canada, Downsview, Ont. Available from http://www.climate.weatheroffice.ec.gc.ca/index.html [accessed on 23 December 2008].

Fleming, T.L., and Freedman, B. 1998. Conversion of natural, mixed-species forests to conifer plantations: implications for dead organic matter and carbon storage. Ecoscience, **5**(2): 213–221.

Fredeen, A.L., Bois, C.H., Janzen, D.T., and Sanborn, P.T. 2005. Comparison of coniferous forest carbon stocks between old-growth and young second-growth forests on two soil types in central British Columbia, Canada. Can. J. For. Res. **35**(6): 1411–1421. doi:10.1139/x05-074.

Gough, C.M., Vogel, C.S., Harrold, K.H., George, K., and Curtis, P.S. 2007. The legacy of harvest and fire on ecosystem carbon storage in a north temperate forest. Glob. Change Biol. **13**(9): 1935–1949. doi:10.1111/j.1365-2486.2007.01406.x.

Gower, S.T., McMurtrie, R.E., and Murty, D. 1996. Aboveground net primary production decline with stand age: potential causes. Trends Ecol. Evol. **11**(9): 378–382. doi:10.1016/0169-5347(96)10042-2.

Gower, S.T., Vogel, J.G., Norman, J.M., Kucharik, C.J., Steele, S.J., and Stow, T.K. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. J. Geophys. Res. Atmos. **102**(D24): 29 029 – 29 041. doi:10.1029/97JD02317.

Gower, S.T., Krankina, O., Olson, R.J., Apps, M., Linder, S., and Wang, C. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl. **11**(5): 1395–1411. doi:10.1890/1051-0761(2001)011[1395:NPPACA]2.0.CO;2.

Hart, S.A., and Chen, H.Y.H. 2006. Understory vegetation dynamics of North American boreal forests. Crit. Rev. Plant Sci. **25**(4): 381–397. doi:10.1080/07352680600819286.

Hart, S.A., and Chen, H.Y.H. 2008. Fire, logging, and overstory affect understory abundance, diversity, and composition in boreal forest. Ecol. Monogr. **78**(1): 123–140. doi:10.1890/06-2140.1.

Howard, E.A., Gower, S.T., Foley, J.A., and Kucharik, C.J. 2004. Effects of logging on carbon dynamics of a jack pine forest in Saskatchewan, Canada. Glob. Change Biol. **10**(8): 1267–1284. doi:10.1111/j.1529-8817.2003.00804.x.

Intergovernmental Panel on Climate Change. 2003. Good practice guidance for land use, land-use change and forestry. Special Report of the Intergovernmental Panel on Climate Change. Institute for Global Environmental Strategies for the IPCC, Hayama, Japan.

Lambert, M.C., Ung, C.H., and Raulier, F. 2005. Canadian national tree aboveground biomass equations. Can. J. For. Res. **35**(8): 1996–2018. doi:10.1139/x05-112.

Legendre, P., and Legendre, L. 1998. Numerical ecology. 2nd ed. Elsevier Science B.V., Amsterdam, Netherlands.

Luyssaert, S., Schulze, E.D., Börner, A., Knohl, A., Hessenmöller, D., Law, B.E., Ciais, P., and Grace, J. 2008. Old-growth forests as global carbon sinks. Nature, **455**(7210): 213–215. doi:10.1038/nature07276. PMID:18784722.

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Magnani, F., Mencuccini, M., Borghetti, M., Berbigier, P., Berninger, F., Delzon, S., Grelle, A., Hari, P., Jarvis, P.G., Kolari, P., Kowalski, A.S., Lankreijer, H., Law, B.E., Lindroth, A., Loustau, D., Manca, G., Moncrieff, J.B., Rayment, M., Tedeschi, V., Valentini, R., and Grace, J. 2007. The human footprint in the carbon cycle of temperate and boreal forests. Nature (Lond.), **447**(7146): 849–851. doi:10.1038/nature05847. PMID: 17568744.

Martin, J.L., Gower, S.T., Plaut, J., and Holmes, B. 2005. Carbon pools in a boreal mixedwood logging chronosequence. Glob. Change Biol. **11**(11): 1883–1894.

Paré, D., and Bergeron, Y. 1995. Above-ground biomass accumulation along a 230-year chronosequence in the southern portion of the Canadian boreal forest. J. Ecol. **83**(6): 1001–1007. doi:10.2307/2261181.

Parker, K.R., and Wiens, J.A. 2005. Assessing recovery following environmental accidents: environmental variation, ecological assumptions, and strategies. Ecol. Appl. **15**(6): 2037–2051. doi:10.1890/04-1723.

Pierce, C.A., Block, R.A., and Aguinis, H. 2004. Cautionary note on reporting eta-squared values from multifactor ANOVA designs. Educ. Psychol. Meas. **64**(6): 916–924. doi:10.1177/0013164404264848.

Pinard, M.A., and Cropper, W.P. 2000. Simulated effects of logging on carbon storage in dipterocarp forest. J. Appl. Ecol. **37**(2): 267–283. doi:10.1046/j.1365-2664.2000.00488.x.

Pregitzer, K.S., and Euskirchen, E.S. 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. Glob. Change Biol. **10**(12): 2052–2077. doi:10.1111/j.1365-2486.2004.00866.x.

Ruel, J.C., Horvath, R., Ung, C.H., and Munson, A. 2004. Comparing height growth and biomass production of black spruce trees in logged and burned stands. For. Ecol. Manage. **193**(3): 371–384. doi:10.1016/j.foreco.2004.02.007.

Ryan, M.G., Binkley, D., and Fownes, J.H. 1997. Age-related decline in forest productivity: pattern and process. Adv. Ecol. Res. **27**: 213–262. doi:10.1016/S0065-2504(08)60009-4.

Ryan, M.G., Binkley, D., Fownes, J.H., Giardina, C.P., and Senock, R.S. 2004. An experimental test of the causes of forest growth decline with stand age. Ecol. Monogr. **74**(3): 393–414. doi:10.1890/03-4037.

Shaw, R.G., and Mitchellolds, T. 1993. ANOVA for unbalanced data — an overview. Ecology, **74**(6): 1638–1645. doi:10.2307/1939922.

Smith, W.B., and Brand, G.J. 1983. Allometric biomass equations for 98 species of herbs, shrubs, and small trees. USDA For. Serv. North Cent. For. Exp. Stn. Res. Note NC-299.

Soil Classification Working Group. 1996. The Canadian system of soil classification. 2nd ed. Agriculture and Agri-Food Canada, Ottawa, Ont. Publ. 1646.

Sprugel, D.G. 1985. Natural disturbance and ecosystem energetics. *In* The ecology of natural disturbance and patch dynamics. *Edited by* S.T.A. Pickett and P.S. White. Academic Press, Orlando, Fla. pp. 335–352.

SPSS Inc.. 2001. SPSS for Windows, version 11.0.0. SPSS Inc., Chicago, Ill.

Steyaert, L.T., Hall, F.G., and Loveland, T.R. 1997. Land cover mapping, fire regeneration, and scaling studies in the Canadian boreal forest with 1 km AVHRR and Landsat TM data. J. Geophys. Res. Atmos. **102**(D24): 29 581 – 29 598. doi:10.1029/97JD01220.

Taylor, A.R., and Chen, H.Y.H. 2010. Multiple successional pathways of boreal forest stands in central Canada. Ecography, **33**. In press. doi:10.1111/j.1600-0587.2010.06455.x.

Taylor, A.R., Wang, J.R., and Chen, H.Y.H. 2007. Carbon storage in a chronosequence of red spruce (*Picea rubens*) forests in central Nova Scotia, Canada. Can. J. For. Res. **37**(11): 2260–2269. doi:10.1139/X07-080.

Taylor, A.R., Wang, J.R., and Kurz, W.A. 2008. Effects of harvesting intensity on carbon stocks in eastern Canadian red spruce (*Picea rubens*) forests: an exploratory analysis using the CBM-CFS3 simulation model. For. Ecol. Manage. **255**(10): 3632–3641. doi:10.1016/j.foreco.2008.02.052.

Taylor, K.C., Arnup, R.W., Meredith, M.P., Parton, W.J., and Nieppola, J. 2000. A field guide to forest ecosystems of northeastern Ontario. 2nd ed. Ontario Ministry of Natural Resources, Northeast Science and Technology, Timmins, Ont. NEST Field Guide FG-01.

Turner, M.G., Romme, W.H., Gardner, R.H., and Hargrove, W.W. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecol. Monogr. **67**(4): 411–433. doi:10.1890/0012-9615(1997)067[0411:EOFSAP]2.0.CO;2.

Vasiliauskas, S., and Chen, H.Y.H. 2002. How long do trees take to reach breast height after fire in northeastern Ontario? Can. J. For. Res. **32**(10): 1889–1892. doi:10.1139/x02-104.

Wang, C.K., Bond-Lamberty, B., and Gower, S.T. 2003. Carbon distribution of a well- and poorly-drained black spruce fire chronosequence. Glob. Change Biol. **9**(7): 1066–1079. doi:10.1046/j.1365-2486.2003.00645.x.

Wang, X.L., Klinka, K., Chen, H.Y.H., and de Montigny, L. 2002. Root structure of western hemlock and western redcedar in single- and mixed-species stands. Can. J. For. Res. **32**(6): 997–1004. doi:10.1139/x02-026.

Weir, J.M.H., Johnson, E.A., and Miyanishi, K. 2000. Fire frequency and the spatial age mosaic of the mixed-wood boreal forest in western Canada. Ecol. Appl. **10**(4): 1162–1177. doi:10.1890/1051-0761(2000)010[1162:FFATSA]2.0.CO;2.

III

Seedre, M., Taylor, A.R., Chen, H.Y.H. and Jõgiste, K. 2013.

DEAD WOOD DENSITY OF FIVE BOREAL TREE SPECIES IN RELATION TO FIELD ASSIGNED DECAY CLASS.

Forest Science 59, 261-266.

Deadwood Density of Five Boreal Tree Species in Relation to Field-Assigned Decay Class

Meelis Seedre, Anthony R. Taylor, Han Y.H. Chen, and Kalev Jõgiste

Abstract: Aboveground deadwood, consisting of downed woody debris (DWD), snags, and stumps, is an important component of boreal forest ecosystem structure. Accurate deadwood density estimates are essential for evaluating ecosystem biomass and carbon stocks. The objective of this study was to examine the relationships between deadwood density, tree species, and decay status, identified in the field by morphological characteristics. We sampled DWD, snags, and stumps of trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.), jack pine (*Pinus banksiana* Lamb.), black spruce (*Picea mariana* [Mill.] B.S.P.), and balsam fir (*Abies balsamea* [L.] Mill.) in the boreal forest of central Canada. A total of 240 samples (99 DWD, 94 snags, and 47 stumps) were collected. Decay class and tree species explained >80% of the variation in wood density of all deadwood types. Wood density decreased consistently from the lowest to the highest decay class. Tree species identity was also important in determining the relationships between wood density and field-assigned decay class for snags and stumps, but not for DWD, probably because of the five-class system used for DWD, rather than the three-class system used for snags and stumps. These results indicate that decay class and tree species are adequate predictors of deadwood density. FOR. SCI. 59(3):261–266.

Keywords: deadwood density, downed woody debris, snags, stumps, decay class

DEADWOOD IS AN IMPORTANT STRUCTURAL COMPONENT of forest ecosystems (Harmon et al. 1986, Brassard and Chen 2006). It contributes to biological diversity (Berglund et al. 2011), carbon storage (Bond-Lamberty et al. 2003), and nutrient cycling (Laiho and Prescott 2004). Accurate measurements of deadwood mass are essential for conducting analyses of ecosystem biomass and carbon budget estimates (Manies et al. 2005, Taylor et al. 2007, Pan et al. 2011).

The aboveground portion of deadwood in forest ecosystems consists of downed woody debris (DWD), snags, and stumps (Brassard and Chen 2006). Sampling deadwood is highly labor intensive, particularly for estimating biomass and carbon content (Larjavaara and Muller-Landau 2010). Consequently, sampling strategies that permit estimation of deadwood density using less intensive methods, such as field-assigned decay class indices, are preferred (Harmon et al. 1987, Pyle and Brown 1998, Naesset 1999).

In much of the boreal and subboreal forest, five decay classes are used to qualify the extent of decay in deadwood (e.g., Manies et al. 2005, Campbell and Laroque 2007); however, three- and four-class systems are also applied (e.g., Martin et al. 2005, Taylor et al. 2007, Sandstrom et al. 2007). In each system, decay class is assigned based on visual and tactile estimation of wood texture and the presence of bark, branches, and twigs (Harmon et al. 1987, Harmon and Sexton 1996, Pyle and Brown 1998).

Decay class is reported to correlate strongly with deadwood density for a number of boreal tree species (Naesset 1999, Yatskov et al. 2003, Sandstrom et al. 2007), indicating that field-estimated decay classes are sufficiently accurate to be used for mass conversion. On the contrary, the degree of decay within a piece of deadwood is typically nonhomogeneous and whole-piece designation into a single decay class can result in high within-class variability, with potential overlap between classes (Pyle and Brown 1999, Eaton and Sanchez 2009). Further, the lack of consistency among classification systems (i.e., differences in decay qualification) can lead to discrepancies in densities among equivalent decay classes (Naesset 1999, Sandstrom et al. 2007), raising questions concerning repeatability over time and space (Larjavaara and Muller-Landau 2010).

Nonetheless, deadwood density is generally considered to decrease with increasing decay class (Harmon et al. 1987, Hale and Pastor 1998, Preston et al. 1998), although different patterns of density decrease have been reported among boreal tree species (Yatskov et al. 2003, Sandstrom et al. 2007, Harmon et al. 2008). In Russian boreal forests, *Betula pendula* (Roth.) exhibited a linear decrease in deadwood density from decay class 1 to 5, whereas species with more decay-resistant heartwood, e.g., *Larix* spp. and some *Pinus* spp., displayed little change in density until decay class 4 (Yatskov et al. 2003). In North American boreal forests, most studies of deadwood decomposition dynamics have

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Table 1. Deadwood classification system for DWD, snags, and stumps.

Type	Decay class	Bark	Wood texture	Cross-sectional shape	Twigs <3 cm (if originally present)
DWD	1	Bark intact	Intact, hard	Round	Twigs present
	2	Intact or partially missing	Intact, hard to partly decaying	Round	No twigs
	3	Trace bark remaining	Large pieces, hard to partly decaying	Round	No twigs
	4	No bark	Small, blocky pieces	Oval to round	No twigs
	5	No bark	Many small pieces, soft portions	Oval	No twigs
Snags and stumps	1	Bark intact	Intact, hard	NA	Twigs present
	2	Bark partially missing to only traces remaining	Hard to partly decaying, some soft portions	NA	No twigs
	3	Trace bark to no bark remaining	Mostly soft portions	NA	No twigs

Classification systems were developed from a modification of Canada's National Forest Inventory Ground Sampling Guidelines (Canadian Forest Inventory Committee 2008) and Harmon and Sexton (1996). Bark characteristics were not used for paper birch because its bark can remain intact while its wood can be highly decayed (Yatskov et al. 2003). NA, not applicable.

focused on decomposition constants (e.g., Alban and Pastor 1993, Bond-Lamberty and Gower 2008), time since death (e.g., Campbell and Laroque 2007, Angers et al. 2010), and residence time within decay classes (e.g., Aakala et al. 2008). Few published studies have examined changes in deadwood density relative to field-assigned decay class or tested the reliability of decay classes as indicators of deadwood density for mass conversion of North American boreal tree species (but see Harmon et al. 2008). Such locally derived estimates of density are important because environmental conditions vary geographically, altering deadwood decomposition dynamics (Alban and Pastor 1993).

Patterns of decay may also vary depending on deadwood position. DWD is reported to decay faster than standing snags because of increased moisture and proximity to decomposing organisms on the forest floor (Mattson et al. 1987, Yatskov et al. 2003). However, the decomposition of stumps is less known, with few studies available to compare stumps with DWD and snag decay dynamics (but see Janisch et al. 2005, Shorohova et al. 2008). In particular, there is a lack of information on stump decay in North American boreal forests, which is of concern, given that stumps contribute a large component of overall deadwood mass after stand-replacing disturbance (Janisch et al. 2005).

In this study, we examine deadwood density of DWD, snags, and stumps in relation to field-assigned decay class for the most common tree species in the central boreal forest of Canada, i.e., trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.), jack pine (*Pinus banksiana* Lamb.), black spruce (*Picea mariana* [Mill.] B.S.P.), and balsam fir (*Abies balsamea* [L.] Mill.). We hypothesize that field-assigned decay class is highly related to deadwood density with density decreasing as decay class increases and also that the relationship between field-assigned decay class and deadwood density varies according to individual boreal tree species.

Materials and Methods

Study Area

This study was conducted in the central boreal forest region of Canada, approximately 150 km north of Thunder Bay, Ontario (49°27′ N to 49°38′ N and 89°29′ W to 89°54′ W). The study area belongs to the Lake Nipigon ecoregion (Ecological Stratification Working Group 1996). This ecoregion surrounds Lake Nipigon and extends westward from the north shore of Lake Superior to Lake St. Joseph in northwestern Ontario. The ecoregion is characterized by warm summers and cold, snowy winters. The average annual temperature is 2.5° C, and average annual precipitation is 712 mm (559 mm rain and 188 mm snow), recorded in Thunder Bay, the closest meteorological station to the study area (Environment Canada 2011).

Sampling

To represent the various types of deadwood, in terms of tree species, decay status, and piece size, samples were collected from a variety of stand types that were of fire origin and some regrown after clearcut harvesting in the vicinity of sample plots previously established by Seedre and Chen (2010). Each deadwood sample for the same species was randomly selected from at least three pieces that were in the same decay class and size class. We sampled DWD, snags, and stumps of trembling aspen, paper birch, jack pine, black spruce, and balsam fir. Because fire-related charring tends to alter the decay dynamics of deadwood (Hagemann et al. 2010), we avoided sampling deadwood with signs of fire damage.

We focused our efforts on coarse deadwood material (>7 cm in diameter). DWD consisted of fallen deadwood, including sound and rotting stems and large branches of various lengths that were non-self-supporting and laying above the soil surface. A five-decay class classification system was used to describe the various stages of decomposition in DWD (Table 1). Snags (self-supporting, standing dead trees ≥1.3 m in height) and stumps (<1.3 m in height) were classified using a three-decay class classification system (Table 1).

Tree species was identified in the field on the basis of bark and wood structure characteristics (US Department of Agriculture 2010). A single decay class was assigned to each DWD, snag, and stump sample based on whether >50% of the sample exemplified the conditions of a single decay class. A disk of approximately 5 cm thickness and ≥7 cm in diameter was then cut from a random location on

Table 2. Density and sample sizes of DWD, snags, and stumps by decay class for major boreal tree species of North America.

Deadwood type	Species	Mean density (SE) and sample sizes for decay class				
		1	2	3	4	5
DWD	Trembling aspen	0.431 (0.026), 3	0.317 (0.027), 4	0.268 (0.019), 3	0.106 (0.011), 4	0.097 (0.011), 3
	Balsam fir	0.386 (0.023), 3	0.359 (0.024), 3	0.199 (0.018), 5	0.153 (0.019), 6	0.143 (0.004), 3
	Paper birch	0.491 (0.013), 3	0.299 (0.050), 6	0.187 (0.013), 5	0.150 (0.016), 4	0.087 (0.010), 4
	Jack pine	0.438 (0.006), 3	0.364 (0.031), 7	0.236 (0.028), 4	0.207 (0.022), 3	0.129 (0.007), 3
	Black spruce	0.438 (0.000), 2	0.353 (0.019), 5	0.208 (0.021), 5	0.193 (0.012), 4	0.115 (0.030), 4
Snags	Trembling aspen	0.369 (0.027), 7	0.285 (0.019), 5	0.252 (0.016), 7		
	Balsam fir	0.329 (0.027), 7	0.319 (0.016), 5	0.234 (0.026), 7		
	Paper birch	0.472 (0.014), 5	0.327 (0.019), 6	0.127 (0.018), 9		
	Jack pine	0.442 (0.014), 6	0.412 (0.017), 6	0.374 (0.020), 6		
	Black spruce	0.463 (0.014), 9	0.342 (0.017), 6	0.210 (0.039), 3		
Stumps	Trembling aspen	0.289 (0.052), 3	0.116 (0.008), 3	0.078 (0.002), 3		
	Balsam fir	0.299 (0.044), 3	0.248 (0.010), 4	0.132 (0.022), 3		
	Paper birch	0.297 (0.024), 4	0.210 (0.025), 3	0.107 (0.005), 3		
	Jack pine	0.442 (0.013), 3	0.349 (0.057), 4	0.187 (0.020), 4		
	Black spruce	0.294 (0.022), 2	0.216 (0.010), 2	0.135 (0.022), 3		

each DWD, snag, and stump sample. Before a disk was cut from a standing snag, it was first felled. For stumps, the upper 5–10 cm of each stump was first removed before a disk was cut. For deadwood samples in advanced stages of decay, diameters at the longest and shortest axis were measured using a timber caliper before a disk was cut to avoid damage from the cutting procedure. An elliptical formula was used to calculate the area. A very high chain saw speed was applied to reduce potential crumbling of the disks during cutting. For each species sampled, we attempted to collect a wide range of disk diameter sizes. A total of 240 samples (99 DWD, 94 snags, and 47 stumps) were collected (Table 2). Diameter of the samples ranged from 7.0 to 29.5, 7.0 to 35.0, and 7.6 to 27.1 cm for DWD, snags, and stumps, respectively. Sampled disks were placed in paper bags and transported to the laboratory for analysis within 48 hours of cutting. Fieldwork was performed in August and October 2008.

Laboratory Analysis

To ensure accurate estimation of sample disk volume, disk thickness and diameter were measured at three locations for each disk. Average thickness and diameter were used to calculate cylinder volume. For disks that were in advanced stages of decay (i.e., decay classes 4 and 5), field-measured diameters were used because these disks tended to break apart during cutting. When present, bark was included as a part of the disk sample. The disks were dried at 70° C until a constant dry mass was achieved (Taylor et al. 2007). Wood density was calculated by dividing sample disk dry mass (g) by volume (cm^3).

Data Analysis

A general linear model was developed for each deadwood type to test the relationship between the response variable (i.e., deadwood density) and a set of explanatory variables (i.e., tree species, piece size diameter, and decay class). Preliminary analysis indicated that piece size diameter was not statistically significant. Therefore, the final models for each deadwood type included only tree species (S; $i = 1, 2, \ldots, 5$) and decay class of DWD (D; $j = 1, 2, \ldots, 5$), snags, and stumps (D; $j = 1, 2, 3$) as covariates.

$$Y_{ijk} = \mu + S_i + D_j + S_i \times D_j + \varepsilon_{(ij)k} \quad (1)$$

where Y_{ijk} is deadwood density and $\varepsilon_{(ij)k}$ is experimental error within tree species and decay class. Assumptions for normality and homogeneity of variances were tested for wood density data, and these assumptions were met without the need of transformation.

For estimation of the proportion of total variance explained by each effect, we calculated percent η^2 values. All statistical analyses were performed in the R software environment (version 2.14.0, 2011; R Development Core Team, Vienna, Austria).

Results

Deadwood density was significantly ($P < 0.001$) related to decay class for all deadwood types (Table 3). Our models explained 86, 82, and 83% of the variation in density for DWD, snags, and stumps, respectively. For all deadwood types, the density decreased consistently from the least

Table 3. Effects of tree species and decay class on deadwood density for DWD, snags, and stumps.

Deadwood type	R^2	Explanatory variables			
		Source	*df*	*P*	η^2 (%)
DWD	0.86	Species	4	0.313	1
		Decay class	4	<0.001	81
		Species × decay class	16	0.208	4
		Error	74		14
Snags	0.82	Species	4	<0.001	26
		Decay class	2	0.002	9
		Species × decay class	8	<0.001	47
		Error	79		18
Stumps	0.83	Species	4	0.005	36
		Decay class	2	0.002	31
		Species × decay class	8	0.413	17
		Error	32		17

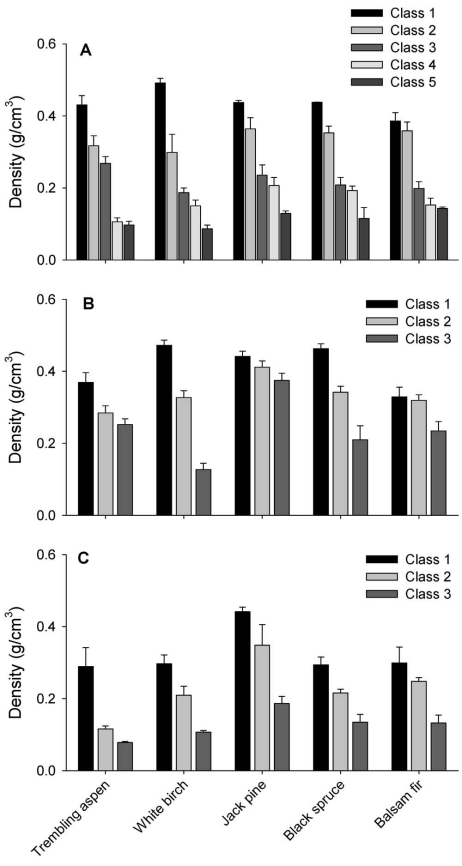

Figure 1. Mean density ($g \cdot cm^{-3}$) (1 SE) of (A) DWD, (B) snags, and (C) stumps by species and decay class.

to the most decayed class (Figure 1). For DWD, decay class explained 81% of total variation in density, whereas tree species only explained 4% (Table 3), indicating that decay class alone is a strong predictor of DWD density.

Tree species and its interaction with decay class explained 26 and 47% of the variation in snag density, respectively (Table 3). Patterns of change in density between decay classes differed among species, with density decreasing the most in paper birch and least in jack pine (Figure 1). For stumps, the interaction between decay class and tree species was not significant ($P > 0.5$), but tree species itself explained 36% of variation in density (Table 3). Jack pine exhibited the highest density values in all decay classes relative to those for other tree species (Figure 1).

Discussion

Our first hypothesis, that field-assigned decay class is highly related to deadwood density, with density decreasing as decay class increases, is strongly supported by our density models for DWD, snags, and stumps. This result is not surprising because many of the visual and tactile characteristics used to assign decay class are indirect assessments of wood density. Although high within-class density variability may arise through whole-piece designation of deadwood into a single decay class (Pyle and Brown 1999), our results suggest that field-assigned decay class is sufficiently reliable as an indicator of density for DWD, snags, and stumps. This observation contradicts findings of Eaton and Sanchez (2009) but corroborates many previous studies undertaken in Scandinavian-Russian boreal forest (e.g., Naesset 1999, Yatskov et al. 2003, Sandstrom et al. 2007, Aakala 2010) and other forest regions (e.g., Sollins 1982, Harmon et al. 1987, Fraver et al. 2002).

Similar to previous reports (e.g., Harmon et al. 1987, Yatskov et al. 2003, Sandstrom et al. 2007), our snag and stump models show that tree species is an important factor explaining variation in deadwood density, providing some support for our second hypothesis, that the relationship between field-assigned decay class and deadwood density varies according to tree species. However, this was not the case for our DWD model in which decay class alone accounted for 81% of the variation in deadwood density. This difference may, in part, be caused by the five-class system applied to DWD compared with the three-class system used for snags and stumps. The greater number of classes further partitions density-related variation in visual and tactile characteristics used to assign decay class, perhaps indicating an advantage to using more classes. However, when comparing five- versus eight-class systems, Naesset (1999) found that both performed equally well. A further explanation for differences of tree species effects between our models may be related to the relatively low sample size captured in our study. Given potential density variation within each decay class, >10 samples per treatment combination may be necessary to detect strong species effects (Pyle and Brown 1999, Campbell and Laroque 2007); however, such replication was not achieved in our study.

Notably, jack pine stumps exhibited the highest density values in all decay classes, and jack pine snags showed a minimal decrease in density from decay class 1 to 3. Other studies have also reported jack pine to be highly decay resistant (e.g., Alban and Pastor 1993, Angers et al. 2010). *Pinus* species generally contain decay-resistant heartwood (Scheffer 1966) and may show little change in density until the final decay class is observed (e.g., decay class 4 or greater) (Yatskov et al. 2003). Because we only used three decay classes, our results do not show the final drop in density that might be expected if we had used five classes. Although trembling aspen and balsam fir are not as decay-resistant as jack pine, snags of these species showed less change in density compared with those for black spruce or paper birch. Correspondingly, Angers et al. (2010) reported that jack pine exhibited longer average lag times before falling, followed by aspen and fir snags, than black spruce snags. However, Aakala et al. (2008) reported slightly lower transition rates between decay classes for black spruce than those for balsam fir. Paper birch snags and stumps exhibited a steeper decay rate than those for other species, similar to

the patterns reported for other *Betula* species (e.g., Yatskov et al. 2003, Shorohova et al. 2008).

Stump density values are, overall, lower than those of snags (Figure 1). Further, stump densities tend to decrease faster than those of snags (e.g., jack pine). Direct comparison between DWD and snags is difficult because of the different decay class systems applied and the common progression from snags to DWD and/or stumps during the decay process. Among decay classes, DWD density also appears to decrease faster than that of snags. This is probably caused by increased moisture conditions on the forest floor and closer proximity to decomposing organisms, which may alter the decomposition process (Mattson et al. 1987, Yatskov et al. 2003, Shorohova et al. 2008). Because snags are suspended in the air, their outer tissues are more susceptible to drying and case hardening (Pyle and Brown 1998, Yatskov et al. 2003). Inner tissues may continue to decompose, but the outer shell remains resistant. Previous studies indicated that DWD decays faster than snags (e.g., Yatskov et al. 2003, Aakala 2010), but ours is the first to indicate this may also be the case for stumps in the boreal forest. This observation conflicts with Janisch et al. (2005), who found no significant difference in decay rates between logs and stumps in *Pseudotsuga menziesii-Thuja heterophylla* forests, but agrees with Shorohova et al. (2008), who suggested that stump decomposition is generally faster than that of suspended deadwood. Although forest carbon budget models often substitute snag decomposition rates for stumps (Janisch et al. 2005, Nalder and Wein 2006, Taylor et al. 2008), different decomposition rates between snags and stumps may affect the assessment of a forest being a carbon sink or source. In further work, use of the exact same classification criteria for the three types of deadwood to test potential differences in wood density among deadwood types may be considered.

Conclusion

By relating field-assessed decay classes and wood density, we showed deadwood density to be highly related to field-assigned decay class in DWD, snags, and stumps in boreal mixedwood forests of central Canada, with density decreasing as decay class increases. Tree species identity was also important in determining the relationships between deadwood density and field-assigned decay class for snags and stumps but not for DWD. This difference between DWD and other deadwood types is probably the result of different numbers of decay classes used. Alternatively, the importance of tree species identity in defining the relationships between wood density and decay classes in snags and stumps may be a result of species-specific responses in drying and case hardening between the bark and inner wood.

Literature Cited

AAKALA, T. 2010. Coarse woody debris in late-successional *Picea abies* forests in northern Europe: Variability in quantities and models of decay class dynamics. *For. Ecol. Manage.* 260(5): 770–779.

AAKALA, T., T. KUULUVAINEN, S. GAUTHIER, AND L. DE GRANDPRE. 2008. Standing dead trees and their decay-class dynamics in the northeastern boreal old-growth forests of Quebec. *For. Ecol. Manage.* 255(3–4):410–420.

ALBAN, D.H., AND J. PASTOR. 1993. Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. *Can. J. For. Res.* 23(9):1744–1749.

ANGERS, V.A., P. DRAPEAU, AND Y. BERGERON. 2010. Snag degradation pathways of four North American boreal tree species. *For. Ecol. Manage.* 259(3):246–256.

BERGLUND, H., J. HOTTOLA, R. PENTTILA, AND J. SIITONEN. 2011. Linking substrate and habitat requirements of wood-inhabiting fungi to their regional extinction vulnerability. *Ecography* 34(5):864–875.

BOND-LAMBERTY, B., AND S.T. GOWER. 2008. Decomposition and fragmentation of coarse woody debris: Re-visiting a boreal black spruce chronosequence. *Ecosystems* 11(6):831–840.

BOND-LAMBERTY, B., C. WANG, AND S.T. GOWER. 2003. Annual carbon flux from woody debris for a boreal black spruce fire chronosequence. *J. Geophys. Res. Atmos* 108(3):WFX-1.

BRASSARD, B.W., AND H.Y.H. CHEN. 2006. Stand structural dynamics of North American boreal forests. *Crit. Rev. Plant. Sci.* 25(2):115–137.

CAMPBELL, L.J., AND C.P. LAROQUE. 2007. Decay progression and classification in two old-growth forests in Atlantic Canada. *For. Ecol. Manage.* 238(1–3):293–301.

CANADIAN FOREST INVENTORY COMMITTEE. 2008. *Canada's national forest inventory ground sampling guidelines*. Available online at cfs.nrcan.gc.ca/pubwarehouse/pdfs/29402.pdf; last accessed Nov. 11, 2011.

EATON, R.J., AND F.G. SANCHEZ. 2009. Quantitative and qualitative measures of decomposition: Is there a link? *South. J. Appl. For.* 33(3):137–141.

ECOLOGICAL STRATIFICATION WORKING GROUP. 1996. *A national ecological framework for Canada.* Agriculture and Agri-Food Canada, Research Branch, Centre for Land and Biological Resources Research, and Environment Canada, State of the Environment Directorate, Ecozone Analysis Branch, Ottawa, ON, Canada. 109 p.

ENVIRONMENT CANADA. 2011. *Canadian climate normals 1981–2010*. Available online at www.climate.weatheroffice.ec.gc.ca/climate_normals/; last accessed June 25, 2011.

FRAVER, S., R.G. WAGNER, AND M. DAY. 2002. Dynamics of coarse woody debris following gap harvesting in the Acadian forest of central Maine, USA. *Can. J. For. Res.* 32(12): 2094–2105.

HAGEMANN, U., M.T. MORONI, J. GLEIßNER, AND F. MAKESCHIN. 2010. Disturbance history influences downed woody debris and soil respiration. *For. Ecol. Manage.* 260(10):1762–1772.

HALE, C.M., AND J. PASTOR. 1998. Nitrogen content, decay rates, and decompositional dynamics of hollow versus solid hardwood logs in hardwood forests of Minnesota, USA. *Can. J. For. Res.* 28(9):1276–1285.

HARMON, M.E., K. CROMACK JR., AND B.G. SMITH. 1987. Coarse woody debris in mixed-conifer forests, Sequoia National Park, California. *Can. J. For. Res.* 17(10):1265–1272.

HARMON, M.E., J.F. FRANKLIN, F.J. SWANSON, P. SOLLINS, S.V. GREGORY, J.D. LATTIN, N.H. ANDERSON, ET AL. 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* 15:133–302.

HARMON, M.E., AND J. SEXTON. 1996. *Guidelines for measurements of woody detritus in forest ecosystems*. US Long Term Ecological Research Network, Publ. 20, Albuquerque, NM.

HARMON, M.E., B. WOODALE, B. FASTH, AND J. SEXTON. 2008. *Woody detritus density and density reduction factors for tree species in the United States: A synthesis*. USDA For. Serv.,

GTR NRS-29, Northern Research Station, Newtown Square, PA.

JANISCH, J.E., M.E. HARMON, H. CHEN, B. FASTH, AND J. SEXTON. 2005. Decomposition of coarse woody debris originating by clearcutting of an old-growth conifer forest. *Ecoscience* 12(2): 151–160.

LAIHO, R., AND C.E. PRESCOTT. 2004. Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: A synthesis. *Can. J. For. Res.* 34(4):763–777.

LARJAVAARA, M., AND H.C. MULLER-LANDAU. 2010. Comparison of decay classification, knife test, and two penetrometers for estimating wood density of coarse woody debris. *Can. J. For. Res.* 40(12):2313–2321.

MANIES, K.L., J.W. HARDEN, B.P. BOND-LAMBERTY, AND K.P. O'NEILL. 2005. Woody debris along an upland chronosequence in boreal Manitoba and its impact on long-term carbon storage. *Can. J. For. Res.* 35(2):472–482.

MARTIN, J.L., S.T. GOWER, J. PLAUT, AND B. HOLMES. 2005. Carbon pools in a boreal mixedwood logging chronosequence. *Global Change Biol.* 11(11):1883–1894.

MATTSON, K.G., W.T. SWANK, AND J.B. WAIDE. 1987. Decomposition of woody debris in a regenerating, clear-cut forest in the Southern Appalachians. *Can. J. For. Res.* 17(7):712–721.

NAESSET, E. 1999. Relationship between relative wood density of *Picea abies* logs and simple classification systems of decayed coarse woody debris. *Scand. J. For. Res.*. 14(5):454–461.

NALDER, I.A., AND R.W. WEIN. 2006. A model for the investigation of long-term carbon dynamics in boreal forests of western Canada: I. Model development and validation. *Ecol. Model.* 192(1–2):37–66.

PAN, Y.D., R.A. BIRDSEY, J.Y. FANG, R. HOUGHTON, P.E. KAUPPI, W.A. KURZ, O.L. PHILLIPS, ET AL. 2011. A large and persistent carbon sink in the world's forests. *Science* 333(6045):988–993.

PRESTON, C.M., J.A. TROFYMOW, J. NIU, AND C.A. FYFE. 1998. ^{13}CPMAS-NMR spectroscopy and chemical analysis of coarse woody debris in coastal forests of Vancouver Island. *For. Ecol. Manage.* 111(1):51–68.

PYLE, C., AND M.M. BROWN. 1998. A rapid system of decay classification for hardwood logs of the eastern deciduous forest floor. *J. Torrey Bot. Soc.* 125(3):237–245.

PYLE, C., AND M.M. BROWN. 1999. Heterogeneity of wood decay classes within hardwood logs. *For. Ecol. Manage.* 114(2–3): 253–259.

SANDSTROM, F., H. PETERSSON, N. KRUYS, AND G. STAHL. 2007. Biomass conversion factors (density and carbon concentration) by decay classes for dead wood of *Pinus sylvestris, Picea abies* and *Betula* spp. in boreal forests of Sweden. *For. Ecol. Manage.* 243(1):19–27.

SCHEFFER, T.C. 1966. Natural resistance of wood to microbial deterioration. *Annu. Rev. Phytopathol.* 4(1):147–168.

SEEDRE, M., AND H.Y.H. CHEN. 2010. Carbon dynamics of aboveground live vegetation of boreal mixedwoods after wildfire and clearcutting. *Can. J. For. Res.* 40(9):1862–1869.

SHOROHOVA, E., E. KAPITSA, AND I. VANHA-MAJAMAA. 2008. Decomposition of stumps in a chronosequence after clear-felling vs. clear-felling with prescribed burning in a southern boreal forest in Finland. *For. Ecol. Manage.* 255(10):3606–3612.

SOLLINS, P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. *Can. J. For. Res.* 12(1):18–28.

TAYLOR, A.R., J.R. WANG, AND H.Y.H. CHEN. 2007. Carbon storage in a chronosequence of red spruce (*Picea rubens*) forests in central Nova Scotia, Canada. *Can. J. For. Res.* 37(11):2260–2269.

TAYLOR, A.R., J.R. WANG, AND W.A. KURZ. 2008. Effects of harvesting intensity on carbon stocks in eastern Canadian red spruce (*Picea rubens*) forests: An exploratory analysis using the CBM-CFS3 simulation model. *For. Ecol. Manage.* 255(10): 3632–3641.

US DEPARTMENT OF AGRICULTURE. 2010. *The PLANTS database*. Available online at plants.usda.gov/java/; last accessed June 25, 2010.

YATSKOV, M., M.E. HARMON, AND O.N. KRANKINA. 2003. A chronosequence of wood decomposition in the boreal forests of Russia. *Can. J. For. Res.* 33(7):1211–1226.

IV

Seedre, M., Taylor, A.R., Brassard, B.W., Chen, H.Y.H., and Jõgiste, K.

TOTAL ECOSYSTEM CARBON DYNAMICS IN YOUNG BOREAL FOREST: COMPARISON OF WILDFIRE AND HARVESTING EFFECTS

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Total ecosystem carbon dynamics in young boreal forest: Comparison of wildfire and harvesting effects.

Running head: Carbon dynamics following harvest versus fire

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Abstract

Corresponding with increasing global resource demand, harvesting now affects millions of hectares of boreal forest each year, yet our understanding of harvesting impacts on boreal C dynamics relative to wildfire remains unclear. We provide a direct comparison of C stocks following clearcut harvesting and fire over a 27-year chronosequence in the boreal forest of central Canada. Although many past studies have lacked measurement of all major C pools, we attempt to provide complete C pool coverage, including live biomass, deadwood, forest floor, and mineral soil C pools. Our results indicate there is no significant difference in overall ecosystem C stocks during early stand development between harvesting and fire. Maximum total ecosystem C was 185.1 ± 18.2 Mg C·ha^{-1} and 163.6 ± 8.0 Mg C·ha^{-1} for harvesting and fire, respectively. However, the relative contribution of each C pool to total ecosystem C varied between disturbance types. Live biomass C was significantly higher following harvesting compared with fire because of residual live trees and advanced regeneration. Conversely, most live biomass was killed following fire, thus post-fire stands contained higher stocks of deadwood C. Snag and stump C mass peaked immediately following fire, but dramatically decreased 8 years after fire as dead trees began to fall over, contributing to the downed woody debris C pool. Our study did not show any initial decrease in forest floor C mass, commonly acknowledged directly after disturbance. Results from this study may be used to further advance our understanding of disturbances in modeling terrestrial C flux.

Key-words: boreal forest, climate change, carbon, disturbance, fire, harvest, productivity

Introduction

The world's boreal forest carbon (C) stocks are increasingly recognized for contributing to the global C cycle and regulating climate change (Pregitzer and Euskirchen 2004; Denman and others 2007; Pan and others 2011). Accurate, empirical estimates of boreal forests C stocks are thus critical to our understanding of global terrestrial C dynamics and the development and validation of reliable C accounting models (Krinner and others 2005; Kull 2011; Stinson and others 2011).

Wildfire is the most prevalent form of stand-replacing disturbance across the circumpolar boreal forest, significantly affecting the capacity of boreal forest to sequester and store C (Stocks 1991; Bond-Lamberty and others 2007). However, corresponding with global trends in resource consumption (Foley and others 2005), millions of hectares of forests are harvested annually (FAO 2010), leading to a significant shift in dominant disturbance regimes. In North America, approximately one million hectares of boreal forest are clearcut each year (Canadian Council of Forest Ministers 2005). Although comparisons of harvested versus fire-originated stands have been made (Seedre and others 2011), evidence of differential disturbance effects is often confounded, as younger harvested stands are compared with older fire-originated stands, naturally indicating greater C stocks in fire-originated forests (e.g., Fredeen and others 2005; Martin and others 2005).

Lack of valid comparisons between post-harvest and post-fire stands largely results from difficulties in finding suitable sample stands of comparable age, predisturbance composition, and site conditions (Martin and others 2005). Furthermore, past studies have often lacked complete measurement of all relevant C pools, including less studied C pools such as tree stumps and

belowground live and dead wood (Gower and others 2001; Janisch and Harmon 2002; Johnson and Miyanishi 2008).

In this study, we provide the first direct comparison of C stocks following clearcut harvesting and stand-replacing wildfire in the boreal forest of central Canada to examine differential disturbance effects on recovery of ecosystem C stocks. We constructed two 27-year chronosequences originating from harvesting and fire disturbances. Changes in C stocks over time can be effectively investigated through the chronosequence approach when supported with strong evidence of developmental histories between sites (Janisch and Harmon 2002; Walker and others 2010; Goulden and others 2011). Our intent was to provide complete empirical estimates of all relevant C pools during early forest development in post-harvest and post-fire stands. More specifically, because most biomass is removed from harvested stands compared with post-fire stands (Rothstein and others 2004; Shrestha and Chen 2010; Thiffault and others 2010), we hypothesize that post-fire stands will contain larger C stocks than post-harvest stands during early stand development (Seedre and others 2011).

Materials and Methods

Study area

Our study was conducted approximately 150 km north of Thunder Bay, Ontario, Canada between 49º27' N to 49º38' N and 89º29' W to 89º54' W at 350–370 m in elevation. This area belongs to the Lake Nipigon Ecoregion and Boreal Shield Ecozone (Ecological Stratification Working Group 1995). This ecoregion surrounds Lake Nipigon and is characterized by warm summers and cold, snowy winters. Mean annual temperature is -1.2 °C and mean annual precipitation is 725 mm (503 mm of rainfall and 253 mm of snow) recorded in Armstrong, Ontario (Environment Canada 2008). Topographic features in this area were shaped by the retreat of the Laurentide Ice Sheet approximately 10 000 years ago. Soils on our sample sites are composed primarily of deep glacial tills of the Brunisolic and Podzolic orders (Shrestha and Chen 2010). Stand-replacing wildfire is the dominant natural disturbance in our study area, with an average fire-return interval of approximately 100 years for the past century (Senici and others, 2010).

Dominant tree species in our study area, in order from least to most shade-tolerant include jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.), black spruce (*Picea mariana* [Mill.] B.S.P), white spruce (*Picea glauca* [Moench] Voss), and balsam fir (*Abies balsamea* [L.] Mill.) (Humbert and others 2007; Seedre and Chen 2010). Common understorey plant species include mountain maple (*Acer spicatum* Lam.), dwarf raspberry (*Rubus pubescens* Raf.), alder (*Alnus* spp.), beaked hazel (*Corylus cornuta* Marsh.), bush honeysuckles (*Diervilla lonicera* Mill.), bluejoint reedgrass (*Calamagrostis canadensis* Michx.), blue-bead lily (*Clintonia borealis* Raf.), Canadian

100 mayflower (*Maianthemum canadense* Desf.), three-leaf goldthread (*Coptis trifolia* Salisb.),
101 violet (*Viola* spp.), and large-leaved aster (*Aster macrophyllus* L.).

102 ***Sampling design***

103 To examine patterns of forest C stocks during early stand development following harvest
104 and fire, we constructed two 27-year chronosequences from stands in our study area that
105 originated from either clearcut harvesting or stand-replacing wildfire. Although the use of the
106 chronosequence method has been criticized because it makes the assumption that sample stands
107 along the temporal sequence have followed the same developmental history (Johnson and
108 Miyanishi 2008), upon careful site selection, replication, and demonstration of developmental
109 links, the chronosequence method is well suited for studying patterns of C dynamics over
110 decadal to centennial time scales (Walker and others 2010).
111 Commercial harvesting only began in our study area in the early 1970s (Shrestha and Chen
112 2010), therefore the temporal scale of our post-harvest and post-fire comparison was limited to
113 available harvested stands from the past 35 years. Our comparison was further constrained by the
114 availability of independent, large, stand-replacing fires that occurred during the same time period
115 as harvesting and within our study area. Nonetheless, we were able to find post-harvest and post-
116 fire stands from three age classes (i.e., 1, 8, and 27 years since disturbance) that coincide with
117 three key developmental stages of stand development in the boreal forest, i.e., stand initiation,
118 late stand initiation, and stem exclusion (Chen and Popadiouk 2002). Similar to Brassard and
119 Chen (2008), dendrochronological evidence from coarse woody debris species, size, and decay
120 attributes, in conjunction with live tree overstorey and understorey species composition, was
121 evaluated to select stands that shared similar developmental histories to provide support for our
122 chronosequence. To minimize the confounding effects of different site conditions, we only chose

123 sites on mesic, flat mid-slope positions with no slope exceeding 5%, which is the dominant site
124 type for boreal mixedwood forest in central Canada. Furthermore, only sites on well-drained
125 glacial moraines, with soils thicker than 50 cm, were selected, which is the prevailing site type in
126 our study area. To verify site suitability, a soil pit was dug in each sample stand and classified
127 according to local ecological classification standards (Taylor and others, 2000). All selected
128 stands had to be at least 1 ha in size and visually homogeneous in structure and tree species
129 composition. To minimize the impact of spatial structure and autocorrelation (Legendre and
130 Legendre 1998; Okland 2007), we avoided sampling stands of the same age class in close
131 proximity to one another. This was achieved by selecting replicate stands from different road
132 access at least 2 km apart. We determined exact stand age (herein referred to as 'time since
133 disturbance', TSD) from local forest fire and harvesting records (Senici and others, 2010)
134 combined with tree coring samples (Hart and Chen 2008). Each stand age class and disturbance
135 origin type (i.e., harvest versus fire) was replicated three times, resulting in a total of 18 sample
136 stands. All fieldwork took place during the summers of 2007 to 2009.

137 ***Data collection***

138 *Aboveground live biomass carbon pool*

139 In each selected sampled stand, we randomly established a 400 m^2 circular plot, within
140 which diameter at breast height (DBH; 1.3 m above the root collar) of all large trees (DBH ≥10
141 cm) was measured. Heights of at least three randomly chosen trees of each species per plot were
142 measured using a TruPulse™ 200 laser range finder. To estimate heights for the remaining trees,
143 a height–diameter curve was developed for each tree species using pooled data for all the
144 sampled stands. The height and DBH of understorey trees (DBH <10 cm, but height >4 m) were

145 measured in a 100 m^2 subplot located within the 400 m^2 main plot. The heights and DBH of
146 saplings and tall shrubs (1.3–4 m in height) were measured in ten 2 x 2 m subplots randomly
147 located within the 400 m^2 main plot.

148 Understorey vascular plant biomass (trees and shrubs <1.3 m in height and herbaceous
149 plants) was estimated by harvesting ten randomly located 1 x 1 m subplots located within the 400
150 m^2 main plot. Plants were clipped at the base and stored in airtight plastic bags and transported
151 daily to the laboratory for determination of mass. Samples were oven dried at 70°C for 48–72 h
152 and weighed. Bryophyte biomass was estimated by harvesting five randomly located 25 x 25 cm
153 subplots located within the 400 m^2 main plot. Furthermore, percent bryophyte coverage was
154 visually estimated for each 400 m^2 main plot. After conversion and scaling of understorey
155 vascular plant and bryophyte biomass to Mg C·ha^{-1}, we combined these two pools as
156 'understorey plants' for our analysis.

157 Aboveground tree biomass was estimated as the sum of stem, branch, and foliage biomass
158 for each tree using published allometric equations (Lambert and others 2005). The biomass of
159 tree components was converted to C assuming C content is 50% of oven-dry wood tissue and
160 45% of foliage tissue (Bisbee and others 2001; Intergovernmental Panel on Climate Change
161 (IPCC) 2003). Carbon content of vascular plants and bryophytes was calculated as 45% of dry
162 biomass (Bisbee and others 2001; IPCC 2003). All aboveground biomass C pools were scaled-up
163 to Mg C·ha^{-1}.

164 *Belowground live biomass carbon pool*

165 Individual coarse root (>10 mm in diameter) biomass estimates were calculated using
166 published allometric root biomass equations based on DBH. For *Pinus banksiana*, *Populus*
167 *tremuloides*, *Picea mariana*, and *Abies balsamea* trees of ≥10 cm DBH, we used locally

168 developed, species-specific equations (Brassard and others 2011a). For *Picea glauca* and *Betula*
169 *papyrifera*, we used the equations for *Picea mariana* and *Populus tremuloides*, respectively,
170 from Brassard and others (2011a). For *Pinus banksiana*, *Populus tremuloides*, *Picea mariana*,
171 and *Betula papyrifera* of <10 cm DBH and *Salix* spp., we used the species-specific equations of
172 Bond-Lamberty and others (2002). For *Picea glauca* and *Abies balsamea*, we used the equation
173 for *Picea mariana*, whereas the equation for *Populus tremuloides* was used for *Acer spicatum*,
174 *Alnus* spp., *Castanea* spp., *Corylus cornuta*, and *Sorbus* spp. As the equations of Bond-Lamberty
175 and others (2002) and Brassard and others (2011a) were developed for small and large
176 individuals, respectively, we decided to use both sets of equations to avoid grossly extrapolating
177 coarse root biomass.
178 Medium (2–10 mm diameter) and fine (<2 mm diameter) root biomass data were collected
179 in 2008 and 2009 from each 400 m^2 circular plot in each sample stand and were determined by
180 soil coring. Within each plot, soil core samples were collected from seven random points
181 following an elongated 'S' pattern every month during July–September in 2008 and May–June
182 2009 with five sampling times in total (we report the average weight of all five measurements to
183 represent growing season average). Soil cores were extracted with a soil corer (6.6 cm in inner
184 diameter) from the forest floor surface to 30 cm depth in the mineral soil using a power auger.
185 The extracted soils were separated into a forest floor layer and two mineral soil sections (0–15
186 cm and 16–30 cm) and transported in an ice-filled cooler to the laboratory, where they were
187 stored at –18°C until processing (Yuan and Chen 2012).
188 In the laboratory, thawed samples were soaked overnight, poured into trays, rubbed gently,
189 and sieved (0.2 mm mesh) to remove roots floating on top of the water. Medium and fine roots
190 were sorted according to vitality (live or dead). Roots were considered 'live' if they were pale

191 colored on the exterior, elastic and flexible, and free of decay with a whitish cortex, whereas
192 roots were classified as 'dead' if they were brown or black in color, rigid and inflexible, in
193 various stages of decay, and had a dark-colored cortex (Brassard and others 2011b). After
194 sorting, roots were oven dried to a constant mass at 65°C and weighed. Live medium and fine
195 root biomass was added to the belowground live biomass pool, and dead fine and medium roots
196 were added to the belowground snag and stump biomass pool, described below. The C content of
197 coarse roots was assumed to be 50% of dry biomass, whereas that of medium and fine roots was
198 assumed to be 45% of dry biomass. All belowground biomass C pools were scaled up to Mg
199 $C \cdot ha^{-1}$.

200 *Aboveground biomass carbon pool of snags and stumps*

201 Snags included both dead trees with and without branches, but their mass was calculated
202 differently. Snags with tops included all trees that appeared dead with no green foliage
203 remaining, were self-supporting, and standing with a zenith angle ≥45 degrees and ≥1.3 m in
204 height. The height and DBH of all those snags (>2 cm DBH) were measured in each 400 m^2 plot.
205 Snag aboveground biomass was estimated similarly to live tree biomass, using collected DBH
206 and height measurements and species-specific allometric equations (Lambert and others 2005);
207 however, to account for loss of bark and branches, all snags were grouped into one of the
208 following three categories and their biomass was reduced accordingly: 1) all bark and branches
209 remaining intact (i.e., no reduction); 2) only 50% of bark and 70% of branches remaining intact;
210 and 3) only 20% of bark and 50% of branches remaining intact.
211 The mass of snags with broken tops and stumps (i.e., snags <1.3 m in height) was
212 estimated as follows. The height and diameter at stem base of all snags and stumps were
213 measured in each 400 m^2 plot and were classified according to locally derived deadwood decay

214 classes (Seedre and others 2013). Snag and stump volume was estimated using a truncated cone
215 formula (Husch and others 2003) and was converted to biomass using site-specific deadwood
216 density values developed by Seedre and others (2013). The C content of all aboveground
217 biomass of snags and stumps was assumed to be 50% of dry biomass (Garrett and others 2012).

218 *Belowground biomass carbon pool of snags and stumps*

219 The biomass of dead coarse roots of snags and stumps was calculated similarly to live
220 coarse roots. However, because the equations of Bond-Lamberty and others (2002) and Brassard
221 and others (2011a) were developed for live trees, dead coarse root biomass estimates had to be
222 adjusted to reflect decay class (Seedre and others 2013). For example, an individual tree that has
223 been dead a long time would have a more decayed coarse root system and less root biomass than
224 an individual with shorter time-since-death. To calculate dead coarse root biomass and account
225 for mass losses due to decay, we used the following equation, which takes advantage of strong
226 correlation between coarse root biomass and density during decay (Olajuyigbe and others 2011)
227 (eq. 1):

228 [1] $$CRB\ (adjusted\ ) = \left(\frac{DW}{LW}\right) \times\ CRB\ (unadjusted\ )$$

229 where *CRB*(*adjusted*) is the coarse root biomass of a dead tree after correcting for losses
230 associated with decay, i.e., an approximate of 'true' dead coarse root biomass, *LW* is the density
231 of the individual assuming it was still alive, *DW* is the density of the individual in its current
232 state of decay, and *CRB*(*unadjusted*) is the coarse root biomass of the individual found using the
233 equations of Bond-Lamberty and others (2002) or Brassard and others (2011a), i.e., calculated as
234 if the individual were still alive. *LW* values were taken from Alemdag (1984), which reports
235 average stemwood density values for live jack pine, aspen, white birch, black spruce, white

spruce, and balsam fir from samples collected in the boreal forest of Ontario, Canada. *DW* values were calculated using local equations from Seedre and others (2013), derived from the same study stands.

Dead medium and fine roots were estimated as described above for belowground live biomass and added to belowground biomass of snags and stumps. The C content of belowground biomass of snags and stumps was assumed to be 50% of dry biomass for coarse roots (Garrett and others, 2012) and 45% of dry biomass for medium and fine roots.

Downed woody debris biomass carbon pool

Downed woody debris (DWD) was defined as all dead wood lying or standing (with a zenith angle ≤45 degrees) with a mid-length diameter ≥2.0 cm and was measured using the line intercept method (Husch and others 2003). Two 50-m transects were established in each sample stand, radiating out from the center of each 400 m^2 circular plot. The first transect was oriented randomly, and the second one was at a 90 degree angle from the first. The diameter at transect, mid-length diameter, species and decay class, according to Seedre and others (2013), of all DWD pieces ≥2.0 cm occurring along the transect were recorded. DWD volume on an area basis was calculated according to Husch and others (2003) (eq. 2):

[2] $$DWD = \frac{\pi^2 \sum d^2}{8L}$$

where d is the piece intercept diameter, and L is the length of the transect. Downed woody debris volume was converted to biomass using site specific deadwood density values developed by Seedre and others (2013). The C content of DWD biomass was assumed to be 50% of dry biomass (Garrett and others 2012) and was scaled up to Mg C·ha^{-1}.

257 *Forest floor and mineral soil carbon pools*

258 Forest floor and mineral soil layer samples were collected from the immediate area
259 surrounding the main 400 m^2 circular plot from six randomly located 40 x 40 cm soil pits. Live
260 moss, lichens, and fresh litter were removed before measuring depth of organic layer and
261 collecting fibric and humus samples. Following excavation of fibric and humus layers, soil core
262 (7.15 cm in diameter and 7.65 cm in height) samples of top mineral soil layers (0–15 and 15–30
263 cm) were collected. Samples were transported back to the lab where they were air dried and
264 sieved (2-mm mesh). We did not collect mineral soil samples >30 cm depth as C stocks in the
265 deep minreal soil were not expected to change significantly following fire throughout the
266 temporal range of our chronosequence (Harden and others 1997; Wirth and others 2002;
267 Goulden and others 2011). Nonetheless, to provide more realistic estimates of total mineral soil
268 C stocks, we used a single average value of deep (30–100 cm) mineral soil C mass derived by
269 Laganière and others (2012) from six local 92-year-old stands from our study area.
270 Bulk density of organic layers was determined by weighing three 10-mL replicates of air-
271 dried, sieved samples (Shrestha and Chen 2010). Mineral soil bulk density was determined by
272 drying in an oven at 105ºC until a constant weight (48 h), and corrected for stone volume.
273 Organic and mineral soil samples were ground in a Wiley mill to measure the physical and
274 chemical parameters. Total organic C was determined by the dry combustion method (McGill
275 and Figueiredo 1993) using LECO CNS 2000, and was scaled up to Mg $C \cdot ha^{-1}$ following
276 methods of Wairiu and Lal (2003).

277 ***Data analysis***

278 All C pools were scaled up to Mg C·ha^{-1} and mean stand-level estimates for each C pool
279 were calculated (Table 1). All C mass data were tested for normality using the *A Shapiro-Wilk*
280 test and for homogeneity of variance using *Levene's* test. Data that were not normally distributed
281 or homogeneous were transformed using a natural logarithm. A two-way analysis of variance
282 (ANOVA) model was used to test if C pool stocks significantly differed with respect to TSD and
283 disturbance types (D).

284 [3] $$Y_{ijk} = \mu + TSD_i + D_j + TSD_i \times D_j + \varepsilon_{(ij)k}$$

285 where TSD is 1, 8 or 27 and Y is C pool mass and ε is experimental error within TSD and D.
286 *Tukey's Honest Significant Difference* method was used for post hoc analysis. All analyses were
287 performed in R 2.15.2 (R Core Team 2012).

288 **Results**

289 Total ecosystem C was related to TSD ($P < 0.05$), but no significant difference could be
290 detected between disturbance types (Table 2). Following harvest, total ecosystem C declined
291 from 146.2 to 127.7 Mg C·ha^{-1}, then increased to 185.1 Mg C·ha^{-1} by year 27 (Table 1, Fig. 1).
292 After fire, total ecosystem C also declined, from 133.8 Mg C·ha^{-1} to 127.6 Mg C·ha^{-1} and
293 reached 163.6 Mg C·ha^{-1} by year 27.

294 The contribution of each C pool to total ecosystem C varied over stand age. Live biomass
295 C generally increased with TSD following harvest and fire (Fig. 2), but a significant interaction
296 effect between TSD and disturbance type was detected ($P < 0.001$, Table 2). Post-harvest stands
297 had significantly higher initial live biomass C compared with post-fire stands, i.e., 15.3 vs. 3.2
298 Mg C·ha^{-1}, respectively. This difference was largely attributable to significant differences in
299 initial aboveground biomass C between post-harvest and post-fire stands (Fig. 3a). Post-harvest
300 stands also had significantly greater live biomass C in the 27-year age class, i.e., 75.1 vs. 23.2
301 Mg C·ha^{-1}, respectively. This divergence is primarily caused by significantly higher
302 aboveground biomass C and coarse root C in the post-harvest stands (Fig. 3a, b). Medium and
303 fine root C significantly increased with TSD, but no significant difference between disturbance
304 types was detected (Table 2; Fig. 3c, d).

305 In both post-harvest and post-fire stands, total deadwood C mass significantly decreased as
306 TSD increased ($P < 0.001$; Table 2), but overall deadwood C mass was significantly higher in
307 post-fire stands (Fig 2b). This difference is largely attributable to aboveground snag and stump C
308 and DWD C mass (Fig. 4a, c). Immediately after disturbance, there is no significant difference in
309 DWD C mass between post-harvest and post-fire stands (Fig. 4c); however, as TSD increases,
310 DWD C significantly increases in post-fire stands to 30.3 Mg C·ha^{-1}, while decreasing in post-

311 harvest stands to 8.0 Mg C·ha^{-1} (Fig 4c). Following this initial divergence, both post-harvest and
312 post-fire stands then show decreases in DWD C mass. Conversely, snag and stump C mass is
313 initially significantly higher in post-fire stands than in post-harvest stands (Fig. 4a); however, as
314 TSD increases, snag and stump C mass significantly decreases in post-fire stands, converging
315 with values observed for post-harvest stands, i.e., approximately 5.0 Mg C·ha^{-1} at year 27. The
316 significant jump in DWD C mass following fire corresponds to the significant drop in snag and
317 stump C mass (Fig. 4a). Belowground snag and stump C mass steadily decreases with TSD
318 following both harvest and fire (Fig. 4b, d) and was significantly higher ($P < 0.005$; Table 2) in
319 post-harvest stands.
320 Forest floor C generally increased during early stand development following harvest and
321 fire (Fig. 2c). Initial forest floor C mass was substantially lower after fire compared with
322 harvesting, i.e., 3.4 vs. 29.2 Mg C·ha^{-1}, respectively, but they become similar by 9 years after
323 disturbance (Table 1, Fig. 2c). Mineral soil C mass appeared to remain relatively stable
324 throughout early stand development following harvest, whereas in post-fire stands, mineral soil
325 C substantially increased by year 27 (Fig. 2d).

Discussion

Our results do not support our original hypothesis that post-fire stands will contain greater C stocks than post-harvest stands during early stand development. Rather, no significant difference could be detected in total ecosystem C stocks between post-harvest and post-fire stands during our 27-year chronosequence. Nonetheless, significant differences were detected in the relative contribution of C pools to total ecosystem C stocks over time between harvested and post-fire stands.

Although live biomass C increased over time in both post-harvest and post-fire stands, harvested stands contained significantly higher live biomass C. This may be explained by the method of clearcut harvesting operations in our study area, where some mature live trees, advanced regeneration (e.g., tree seedlings and saplings), and shrubs and herbs are left intact to promote regeneration and provide residual wildlife habitat (Ilisson and Chen 2009). On the contrary, our post-fire sites experienced intense crown fire, and all live biomass was almost completely consumed, cf., Fig. 5a, b (Seedre and Chen 2010). Therefore, the live biomass C pool in the post-harvest stands had a "head-start" compared with our post-fire stands, where live biomass C stocks essentially start from zero. However, under less intense fire conditions more live biomass can remain intact (Johnstone and Kasischke 2005; Kovaleva and Ivanova 2013)

Deadwood C stocks decreased over time and were significantly higher in post-fire stands. Although most tree stems are removed from the stand during clearcut harvesting, post-fire stems are often left intact following fire as burnt snags (Fig. 5a, b), even under intense crown fire conditions (Kashian and others 2006). This is particularly evident from the initial high snag and stump C stocks in post-fire stands shown in Fig. 4a and Fig 5a. Interestingly, following this initial peak in snag and stump C mass in post-fire stands, snag and stump C mass dramatically

decreases 8 years after fire, as snags fall down with time (Angers and others 2011). This is supported by Fig. 4c, which shows a correspondingly sharp increase in DWD C stocks 8 years after fire, suggesting a large flux of C mass from standing deadwood to the DWD C pool.

Forest floor C stocks steadily increased throughout early stand development in post-harvest and post-fire stands. Although long-term (>20 years) increases in forest floor C mass are expected after stand-replacing disturbance (Covington 1981; Pregitzer and Euskirchen 2004), our results did not show the typical early decrease in forest floor C mass commonly acknowledged after stand-replacing disturbance, whereby rate of decomposition exceeds rate of litter production (Covington 1981; Wang and others 2003; Yanai and others 2003a; Rothstein and others 2004). This may be because fire intensity was high in our post-fire stands and most forest floor biomass was consumed (e.g., Yanai and others 2003b; Certini 2005; Shrestha and Chen 2010). In harvested sites, the decline may have happened before the year 8 measurement took place. Although no statistically significant difference between post-harvest and post-fire forest floor C stocks was detected in our study, a marginal effect is evident in Fig. 2c, in which substantially more forest floor C mass is present directly following harvesting compared with fire. Differences in forest floor mass after harvest and intense fire are inherent as a lot of debris is created during harvest operations contrary to nearly complete consumption of forest floor material by stand-replacing wildfire (Yanai and others 2003b; Neff and others 2005; Shrestha and Chen 2010). However, as TSF increases, it appears forest floor C stocks in post-harvest and post-fire stands begin to converge.

Our results indicate mineral soil C stocks remained relatively stable throughout early stand development following harvesting, similar to previous studies that have examined disturbance impacts on boreal forest soil development (Harden and others 2000; Johnson and Curtis 2001;

372 Wirth and others 2002; Chen and Shrestha 2012). Changes in mineral soil C are often difficult to
373 detect given large, natural variation among stands (Pregitzer and Euskirchen 2004). Furthermore,
374 studies have found harvesting and fire do not drastically affect mineral soil C stocks (Johnson
375 and Curtis 2001). Nonetheless, our results show that mineral soil C was initially higher in post-
376 harvest stands, suggesting that the intense crown fire experienced by our post-fire stands may
377 have resulted in some mineral soil C loss from the system (e.g., Bormann and others, 2008).
378 However, this is difficult to confirm as pre-disturbance soil C data are not available. A
379 significant increase in mineral soil C 27 years after fire indicates potential incorporation of fire-
380 created debris into the mineral soil C pool (Pregitzer and Euskirchen 2004; Seedre and others
381 2011). Conversely, lack of significant increase in post-harvest mineral soil C suggests slower
382 incorporation of disturbance-created debris.
383 Our results suggest common forest management practices in the boreal forest (i.e., clearcut
384 harvesting followed by planting or natural regeneration) may have little impact on total
385 ecosystem C stocks in young forest compared with wildfire. Furthermore, when considering the
386 life cycle of wood products acquired from harvesting and their potential displacement effects
387 (i.e., use of wood instead of concrete or steel), harvesting of wood products may actually result
388 in increased C uptake from the atmosphere, relative to wildfire, and provide potential climate
389 change mitigation effects (Gower 2003; Sathre and O'Connor 2010; Lippke and others 2011).
390 However, longer-term studies that compare C stocks throughout late stand development will be
391 required to confirm such hypotheses.

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401 **References**

402 Alemdag IS. 1984. Wood density variation of 28 tree species from Ontario. Natural Resources
403 Canada, Canadian Forest Service - Petawawa National Forestry Institute, Chalk River,
404 Ontario, Canada.

405 Angers VA, Gauthier S, Drapeau P, Jayen K, Bergeron Y. 2011. Tree mortality and snag
406 dynamics in North American boreal tree species after a wildfire: a long-term study.
407 International Journal of Wildland Fire 20: 751–763.

408 Bisbee KE, Gower ST, Norman JM, Nordheim EV. 2001. Environmental controls on ground
409 cover species composition and productivity in a boreal black spruce forest. Oecologia 129:
410 261–270.

411 Bond-Lamberty B, Peckham SD, Ahl DE, Gower ST. 2007. Fire as the dominant driver of
412 central Canadian boreal forest carbon balance. Nature 450: 89-92.

413 Bond-Lamberty B, Wang C, Gower ST. 2002. Aboveground and belowground biomass and
414 sapwood area allometric equations for six boreal tree species of northern Manitoba. Canadian
415 Journal of Forest Research 32: 1441-1450.

416 Bormann BT, Homann PS, Darbyshire RL, Morrissette BA. 2008. Intense forest wildfire
417 sharply reduces mineral soil C and N: the first direct evidence. Canadian Journal of Forest
418 Research 38: 2771-2783.

419 Brassard BW, Chen HYH. 2008. Effects of forest type and disturbance on diversity of coarse
420 woody debris in boreal forest. Ecosystems 11: 1078-1090.

421 Brassard BW, Chen HYH, Bergeron Y, Paré D. 2011a. Coarse root biomass allometric
422 equations for *Abies balsamea , Picea mariana, Pinus banksiana* , and *Populus tremuloide*s
423 in the boreal forest of Ontario, Canada. Biomass and Bioenergy 35: 4189-4196.

424 Brassard BW, Chen HYH, Bergeron Y, Paré D. 2011b. Differences in fine root productivity
425 between mixed- and single-species stands. Functional Ecology 25: 238-246.
426 Canadian Council of Forest Ministers. 2005. Criteria and indicators of sustainable forest
427 management in Canada-National status 2005, Natural Resources Canada, Canadian Forest
428 Service, Ottawa, Ontario, Canada.
429 Certini G. 2005. Effects of fire on properties of forest soils: a review. Oecologia 143, 1-10.
430 Chen HYH, Popadiouk RV. 2002. Dynamics of North American boreal mixedwoods.
431 Environmental Reviews 10: 137-166.
432 Chen HYH, Shrestha BM. 2012. Stand age, fire and clearcutting affect soil organic carbon
433 and aggregation of mineral soils in boreal forests. Soil Biology & Biochemistry 50: 149-157.
434 Covington WW. 1981. Changes in Forest Floor Organic Matter and Nutrient Content
435 Following Clear Cutting in Northern Hardwoods. Ecology 62: 41-48.
436 Denman KL, Brasseur G, Chidthaisong A, Ciais P, Cox PM, Dickinson RE, Hauglustaine D,
437 Heinze C, Holland E, Jacob D. 2007. Couplings between changes in the climate system and
438 biogeochemistry. Climate change 2007: 541-584.
439 Ecological Stratification Working Group. 1995. A national ecological framework for Canada.
440 Agriculture and Agrifood Canada, Research Branch, Center for Land and Biological
441 Resources Research and Environment Canada, State of the Environment, Directorate,
442 Ecozone Analysis Branch, Ottawa/Hull. 125 p.
443 Environment Canada. 2008. Climate normals for Thunder Bay, ON, Canada (1971–2000)
444 [online]. Environment Canada, Meteorological Service of Canada, Downsview, Ontario.
445 http://www.climate.weatheroffice.ec.gc.ca/index.html
446 FAO. 2010. Global Forest Resources Assessment 2010: Main Report. Food and Agriculture
447 Organization of the United Nations, Rome.

448 Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT,
449 Daily GC, Gibbs HK, Helkowski JH, Holloway T, Howard EA, Kucharik CJ, Monfreda C,
450 Patz JA, Prentice IC, Ramankutty N, Snyder PK. 2005. Global consequences of land use.
451 Science 309: 570-574.
452 Fredeen AL, Bois CH, Janzen DT, Sanborn PT. 2005. Comparison of coniferous forest carbon
453 stocks between old-growth and young second-growth forests on two soil types in central
454 British Columbia, Canada. Canadian Journal of Forest Research 35: 1411-1421.
455 Garrett LG, Kimberley MO, Oliver GR, Pearce SH, Beets PN. 2012. Decomposition of coarse
456 woody roots and branches in managed *Pinus radiata* plantations in New Zealand: a time
457 series approach. Forest Ecology and Management 269: 116-123.
458 Goulden ML, McMillan AMS, Winston GC, Rocha AV, Manies KL, Harden JW, Bond-
459 Lamberty BP. 2011. Patterns of NPP, GPP, respiration, and NEP during boreal forest
460 succession. Global Change Biology 17: 855-871.
461 Gower ST. 2003. Patterns and mechanisms of the forest carbon cycle. Annual Review of
462 Environment and Resources 28: 169-204.
463 Gower ST, Krankina O, Olson RJ, Apps M, Linder S, Wang C. 2001. Net primary production
464 and carbon allocation patterns of boreal forest ecosystems. Ecological Applications 11: 1395-
465 1411.
466 Harden JW, O'Neill KP, Trumbore SE, Veldhuis H, Stocks BJ. 1997. Moss and soil
467 contributions to the annual net carbon flux of a maturing boreal forest. Journal of Geophysical
468 Research-Atmospheres 102: 28805-28816.
469 Harden JW, Trumbore SE, Stocks BJ, Hirsch A, Gower ST, O'Neill KP, Kasischke ES. 2000.
470 The role of fire in the boreal carbon budget. Global Change Biology 6: 174-184.
471 Hart SA, Chen HYH. 2008. Fire, logging, and overstory affect understory abundance,
472 diversity, and composition in boreal forest. Ecological Monographs 78: 123-140.

473 Humbert L, Gagnon D, Kneeshaw D, Messier C. 2007. A shade tolerance index for common
474 understory species of northeastern North America. Ecological Indicators 7: 195-207.
475 Husch B, Beers TW, Kershaw JA. 2003. Forest Mensuration. John Wiley & Sons, Inc. New
476 Jersey. 443 p.
477 Ilisson T, Chen HYH. 2009. Response of Six Boreal Tree Species to Stand Replacing Fire and
478 Clearcutting. Ecosystems 12: 820-829.
479 Intergovernmental Panel on Climate Change (IPCC). 2003. Good practice guidance for land
480 use, land-use change and forestry. Special Report, Intergovernmental Panel on Climate
481 Change. Institute for Global Environmental Strategies for the IPCC, Hayama, Japan.
482 Janisch JE, Harmon ME. 2002. Successional changes in live and dead wood carbon stores:
483 Implications for net ecosystem productivity. Tree Physiology 22: 77-89.
484 Johnson DW, Curtis PS. 2001. Effects of forest management on soil C and N storage: meta
485 analysis. Forest Ecology and Management 140: 227-238.
486 Johnson EA, Miyanishi K. 2008. Testing the assumption of chronosequences in succession.
487 Ecology Letters 11: 1-13.
488 Johnstone JF, Kasischke ES. 2005. Stand-level effects of soil burn severity on postfire
489 regeneration in a recently burned black spruce forest. Canadian Journal of Forest Research 35:
490 2151-2163.
491 Kashian DM, Romme WH, Tinker DB, Turner MG, Ryan MG. 2006. Carbon storage on
492 landscapes with stand-replacing fires. Bioscience 56: 598-606.
493 Kovaleva NM, Ivanova GA. 2013. Recovery of ground vegetation at the initial stage of fire
494 succession. Contemporary Problems of Ecology 6: 162-169.
495 Krinner G, Viovy N, de Noblet-Ducoudre N, Ogee J, Polcher J, Friedlingstein P, Ciais P,
496 Sitch S, Prentice IC. 2005. A dynamic global vegetation model for studies of the coupled
497 atmosphere-biosphere system. Global Biogeochemical Cycles DOI: 10.1029/2003GB002199

498 Kull SJ, Rampley GJ, Morken S, Metsaranta JM, Neilson ET, Kurz WA. 2011. Operational-
499 scale carbon budget model of the Canadian forest sector (CBM-CFS3) version 1.2: user's
500 guide. 2011, Natural Resources Canada, Canadian Forest Service - Northern Forestry Centre,
501 Edmonton, Alberta.
502 Laganière J, Paré D, Bergeron Y, Chen HYH. 2012. The effect of boreal forest composition
503 on soil respiration is mediated through variations in soil temperature and C quality. Soil
504 Biology and Biochemistry 53: 18-27.
505 Lambert MC, Ung CH, Raulier F. 2005. Canadian national tree aboveground biomass
506 equations. Canadian Journal of Forest Research 35: 1996-2018.
507 Legendre P, Legendre L. 1998. Numerical ecology. Elsevier, Amsterdam ; New York.
508 Lippke B, Oneil E, Harrison R, Skog K, Gustavsson L, Sathre R. 2011. Life cycle impacts of
509 forest management and wood utilization on carbon mitigation: knowns and unknowns.
510 Carbon Management 2: 303-333.
511 Martin JL, Gower ST, Plaut J, Holmes B. 2005. Carbon pools in a boreal mixedwood logging
512 chronosequence. Global Change Biology 11: 1883-1894
513 McGill MB, Figueiredo CT. 1993. Soil sampling and methods of analysis. Carter MR editors.
514 *Soil sampling and methods of analysis*, Lewis, Boca Raton. p209-211.
515 Neff JC, Harden JW, Gleixner G. 2005. Fire effects on soil organic matter content,
516 composition, and nutrients in boreal interior Alaska. Canadian Journal of Forest Research 35:
517 2178-2187.
518 Okland RH. 2007. Wise use of statistical tools in ecological field studies. Folia Geobot 42:
519 123-140.
520 Olajuyigbe SO, Tobin B, Gardiner P, Nieuwenhuis M. 2011. Stocks and decay dynamics of
521 above- and belowground coarse woody debris in managed Sitka spruce forests in Ireland.
522 Forest Ecology and Management 262: 1109-1118.

523 Pan YD, Birdsey RA, Fang JY, Houghton R, Kauppi PE, Kurz WA, Phillips OL, Shvidenko
524 A, Lewis SL, Canadell JG, Ciais P, Jackson RB, Pacala SW, McGuire AD, Piao SL,
525 Rautiainen A, Sitch S, Hayes D. 2011. A Large and Persistent Carbon Sink in the World's
526 Forests. Science 333: 988-993.
527 Pregitzer KS, Euskirchen ES. 2004. Carbon cycling and storage in world forests: biome
528 patterns related to forest age. Global Change Biology 10: 2052-2077.
529 R Core Team. 2012. R: A language and environment for statistical computing, R Foundation
530 for Statistical Computing, Vienna, Austria. http://www.R-project.org.
531 Rothstein. DE, Yermakov Z, Buell AL. 2004. Loss and recovery of ecosystem carbon pools
532 following stand-replacing wildfire in Michigan jack pine forests. Canadian Journal of Forest
533 Research 34: 1908-1918.
534 Sathre R, O'Connor J. 2010. Meta-analysis of greenhouse gas displacement factors of wood
535 product substitution. Environmental Science and Policy 13: 104-114.
536 Seedre M, Chen HYH. 2010. Carbon dynamics of aboveground live vegetation of boreal
537 mixedwoods after wildfire and clear-cutting. Canadian Journal of Forest Research 40: 1862-
538 1869.
539 Seedre M, Shrestha BM, Chen HYH, Colombo S, Jogiste K. 2011. Carbon dynamics of North
540 American boreal forest after stand replacing wildfire and clearcut logging. Journal of Forestry
541 Research. 16: 168-183.
542 Seedre M, Taylor AR, Chen HYH, Jogiste K. 2013. Dead wood density of five boreal tree
543 species in relation to field assigned decay class. Forest Science 59: 261-266.
544 Senici D, Chen HYH, Bergeron Y, Cyr D. 2010. Spatiotemporal Variations of Fire Frequency
545 in Central Boreal Forest. Ecosystems 13: 1227-1238.
546 Shrestha BM, Chen HYH. 2010. Effects of stand age, wildfire and clearcut harvesting on
547 forest floor in boreal mixedwood forests. Plant and Soil 336: 267-277.

548 Stinson G, Kurz WA, Smyth CE, Neilson ET, Dymond CC, Metsaranta JM, Boisvenue C,
549 Rampley GJ, Li Q, White TM, Blain D. 2011. An inventory-based analysis of Canada's
550 managed forest carbon dynamics, 1990 to 2008. Global Change Biology 17: 2227-2244.
551 Stocks BJ. 1991. The extent and impact of forest fires in northern circumpolar countries.
552 Levine JS editor. Global Biomass Burning: Atmospheric, Climatic, and Biospheric
553 Implications. The MIT Press, Cambridge MA. p197-202.
554 Taylor KC, Arnup RW, Meredith MP, Parton WJ, Nieppola J. 2000. Field Guide to Forest
555 Ecosystems of Northeastern Ontario 2 edn. NEST Field Guide FG-01, Northeast Science and
556 Technology, Ontario Ministry of Natural Resources, Timmins, Ontario, Canada.
557 Thiffault E, Paré D, Brais S, Titus BD. 2010. Intensive biomass removals and site
558 productivity in Canada: A review of relevant issues. Forestry Chronicle 86: 36-42.
559 Wairiu M, Lal R. 2003. Soil organic carbon in relation to cultivation and topsoil removal on
560 sloping lands of Kolom-bangara, Solomon Islands. Soil and Tillage Research 70: 19-27
561 Walker LR, Wardle DA, Bardgett RD, Clarkson BD. 2010. The use of chronosequences in
562 studies of ecological succession and soil development. Journal of Ecology 98: 725-736.
563 Wang CK, Bond-Lamberty B, Gower ST. 2003. Carbon distribution of a well- and poorly-
564 drained black spruce fire chronosequence. Global Change Biology 9: 1066-1079.
565 Wirth C, Schulze ED, Lühker B, Grigoriev S, Siry M, Hardes G, Ziegler W, Backor M, Bauer
566 G, Vygodskaya NN. 2002. Fire and site type effects on the long-term carbon and nitrogen
567 balance in pristine Siberian Scots pine forests. Plant Soil 242: 41-63.
568 Yanai RD, Currie WS, Goodale CL. 2003a. Soil carbon dynamics after forest harvest: An
569 ecosystem paradigm reconsidered. Ecosystems 6: 197-212.
570 Yanai RD, Stehman SV, Arthur MA, Prescott CE, Friedland AJ, Siccama TG, Binkley D.
571 2003b. Detecting change in forest floor carbon. Soil Science Society of America Journal 67:
572 1583-1593.

573 Yuan ZY, Chen HYH. 2012. Fine root dynamics with stand development in the boreal forest.
574 Functional Ecology 26: 991-998.

Table legend

Table 1. Ecosystem C stock distribution (Mg C·ha^{-1}) after harvesting and wildfire over a 27-year chronosequence.

Table 2. Time since disturbance (TSD), disturbance type, and their interaction effects on ecosystem C pools.

581 **Table 1**

	Age class											
	1				8				27			
C Pool	**cut**		**fire**		**cut**		**fire**		**cut**		**fire**	
Live Aboveground Vegetation												
Large trees (>10cm DBH)	8.4	(2.1)	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)	48.0	(3.0)	1.0	(0.3)
Small trees (<10cm DBH)	0.0	(0.0)	0.0	(0.0)	2.4	(0.0)	3.1	(1.3)	3.7	(1.7)	12.2	(1.6)
Herbs and Shrubs	0.0	(0.0)	0.1	(0.0)	0.2	(0.0)	0.3	(0.1)	0.3	(0.1)	0.1	(0.1)
Bryophytes	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)	0.2	(0.1)	0.3	(0.1)
Live Belowground Vegetation												
Coarse roots (≥10 mm)	2.3	(0.5)	0.0	(0.0)	0.7	(0.1)	0.7	(0.2)	15.7	(0.9)	2.4	(0.3)
Medium and fine roots (<10 mm)	4.5	(0.3)	3.1	(0.4)	4.6	(1.5)	5.2	(0.2)	7.2	(1.0)	7.3	(0.6)
Total Live Vegetation	**15.3**	**(2.8)**	**3.2**	**(0.4)**	**7.8**	**(1.6)**	**9.4**	**(1.3)**	**75.1**	**(4.3)**	**23.2**	**(1.7)**
Dead Vegetation												
Aboveground snags and stumps	1.2	(0.2)	47.9	(4.3)	5.3	(0.8)	7.7	(2.7)	4.1	(1.3)	1.0	(0.3)
Coarse roots (≥10 mm)	21.7	(2.5)	18.3	(1.8)	20.6	(3.6)	8.8	(0.5)	6.8	(3.2)	2.4	(0.9)
Medium and fine roots (<10 mm)	2.1	(0.4)	1.2	(0.2)	1.4	(0.3)	0.8	(0.3)	0.6	(0.0)	1.0	(0.4)
Downed woody debris	14.8	(0.4)	9.6	(1.0)	8.0	(1.4)	30.3	(5.6)	1.6	(0.7)	21.5	(4.3)
Total Dead Vegetation	**39.8**	**(2.1)**	**77.0**	**(6.1)**	**35.4**	**(5.7)**	**47.6**	**(2.9)**	**13.2**	**(4.9)**	**25.9**	**(2.9)**
Forest floor	**29.2**	**(2.7)**	**3.4**	**(0.9)**	**27.7**	**(9.2)**	**26.9**	**(8.6)**	**41.4**	**(6.9)**	**50.2**	**(8.7)**
Mineral Soil (0–100 cm)												
Top layer (0–30 cm)	38.7	(3.0)	27.0	(1.3)	33.6	(4.9)	20.5	(1.3)	32.3	(4.7)	41.1	(5.5)
Lower layer (31–100 cm)	23.2	(0.0)	23.2	(0.0)	23.2	(0.0)	23.2	(0.0)	23.2	(0.0)	23.2	(0.0)
Total Mineral Soil	**61.8**	**(3.0)**	**50.2**	**(1.3)**	**56.8**	**(4.9)**	**43.7**	**(1.3)**	**55.5**	**(4.7)**	**64.3**	**(5.5)**
Total Ecosystem C	**146.2**	**(7.2)**	**133.8**	**(5.9)**	**127.7**	**(19.2)**	**127.6**	**(8.7)**	**185.1**	**(18.2)**	**163.6**	**(8.0)**

582 * Numbers in parentheses are ± 1 SE (n = 3).

118

583 **Table 2**

C Pool	TSD (df=2) F	TSD (df=2) *P*	D (df = 1) F	D (df = 1) *P*	TSD x D (df = 2) F	TSD x D (df = 2) *P*
Live biomass C						
Aboveground biomass *	134.3	**<0.001**	83.3	**<0.001**	30.3	**<0.001**
Coarse roots *	162.3	**<0.001**	147.0	**<0.001**	38.1	**<0.001**
Medium roots	12.1	**0.001**	0.3	0.589	3.6	**0.060**
Fine roots *	9.5	**0.003**	0.0	0.887	0.2	0.828
Total roots	40.6	**<0.001**	17.5	**0.001**	8.7	**0.005**
Total biomass *	110.0	**<0.001**	58.0	**<0.001**	22.4	**<0.001**
Dead biomass C						
Aboveground snags and stumps*	14.9	**0.002**	10.0	**0.007**	31.5	**<0.001**
DWD	4.0	**0.047**	25.5	**<0.001**	13.0	**<0.001**
Dead coarse roots	21.5	**<0.001**	11.3	**0.006**	1.9	0.198
Dead medium and fine roots *	9.2	**0.009**	2.2	0.161	5.4	**0.035**
Total dead roots	22.7	**<0.001**	12.0	**0.005**	1.9	0.185
Total dead wood	39.6	**<0.001**	33.5	**<0.001**	5.3	**0.022**
Forest floor and mineral soil C						
Forest floor	9.2	**0.004**	1.1	0.317	3.3	**0.071**
Mineral soil	3.2	**0.077**	2.9	0.115	5.1	**0.025**
Total ecosystem C						
Total ecosystem	7.6	**0.007**	1.3	0.285	0.4	0.697

584

585 *transformed data

586 Note: Significant ($p < 0.05$) and marginally significant ($p = 0.06$ - 0.1) values are in bold.

Figure legend

Figure 1:

Total ecosystem C after harvest and fire in relation to time since disturbance (TSD). Symbols represent stand means for each age class (± 1 SE; $n = 3$).

(Note: Different letters indicate significant difference based on effects of TSD)

Figure 2:

Main C pools after harvest and fire in relation to time since disturbance (TSD) for a) Live biomass; b) Deadwood; c) Forest floor; and d) Mineral soil (0–100cm). Symbols represent stand means for each age class (± 1 SE; $n = 3$).

(Note: Different letters indicate significant difference)

Figure 3:

Live biomass C pools after harvest and fire in relation to time since disturbance (TSD) for a) Aboveground biomass; b) Coarse roots; c) Medium roots; and d) Fine roots. Symbols represent stand means for each age class (± 1 SE; $n = 3$).

(Note: Different letters indicate significant difference)

Figure 4:

Deadwood C pools after harvest and fire in relation to time since disturbance (TSD) for a) Snag and stump aboveground biomass; b) Snag and stump coarse roots c) Downed woody debris (DWD); and d) Dead medium and fine roots. Symbols represent stand means for each age class (± 1 SE; $n = 3$).

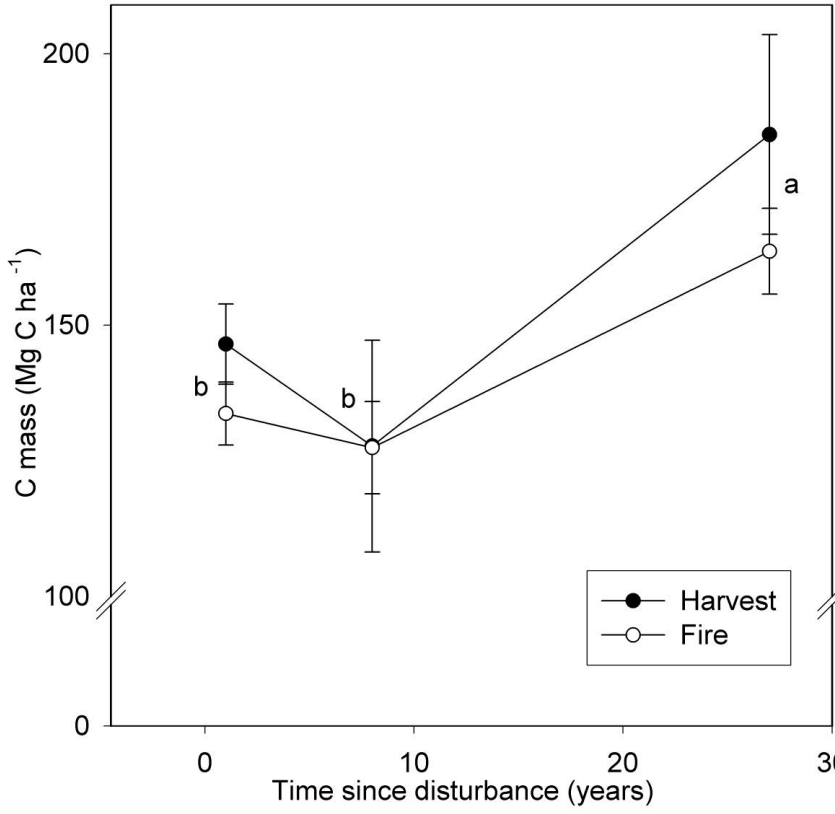
(Note: different letters indicate significant difference. Y axes are different in graphs c and d.)

612 **Figure 5:**

613 Photographs showing a: a) post-fire stand, and a b) post-harvest stand from our study area

614 approximately 1 year after disturbance.

615 **Figure 1**



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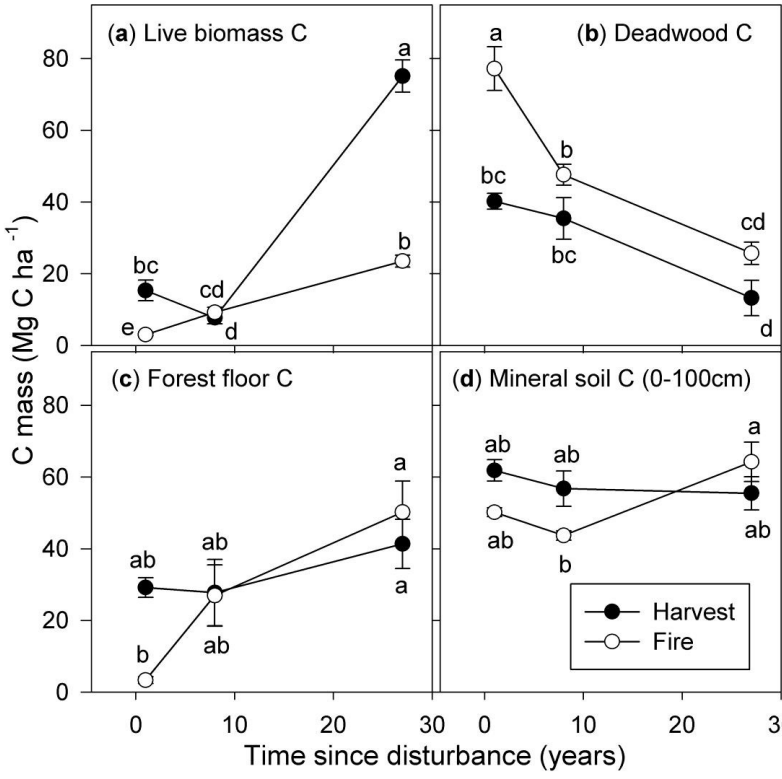
618 **Figure 2**



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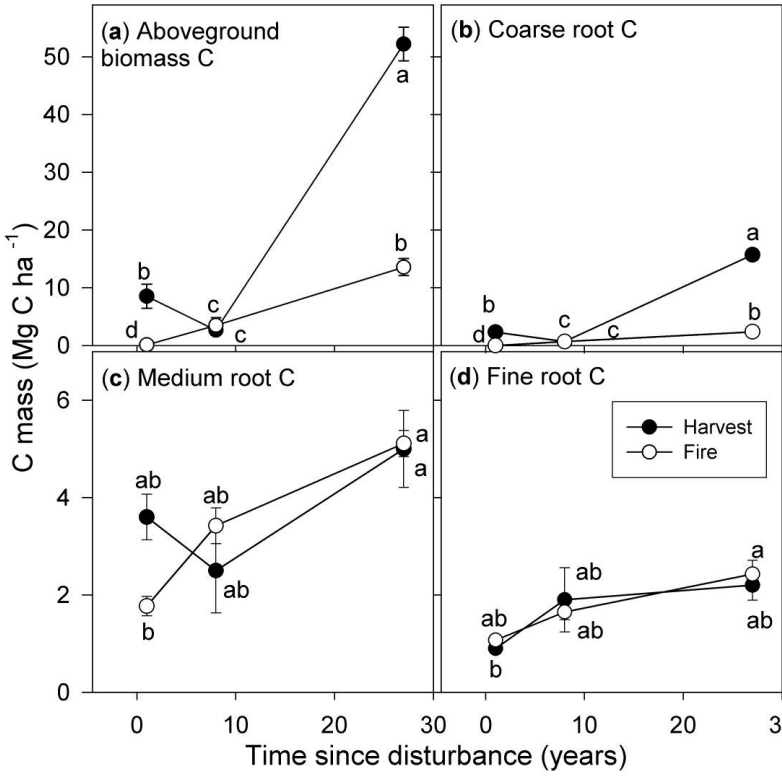
621 **Figure 3**



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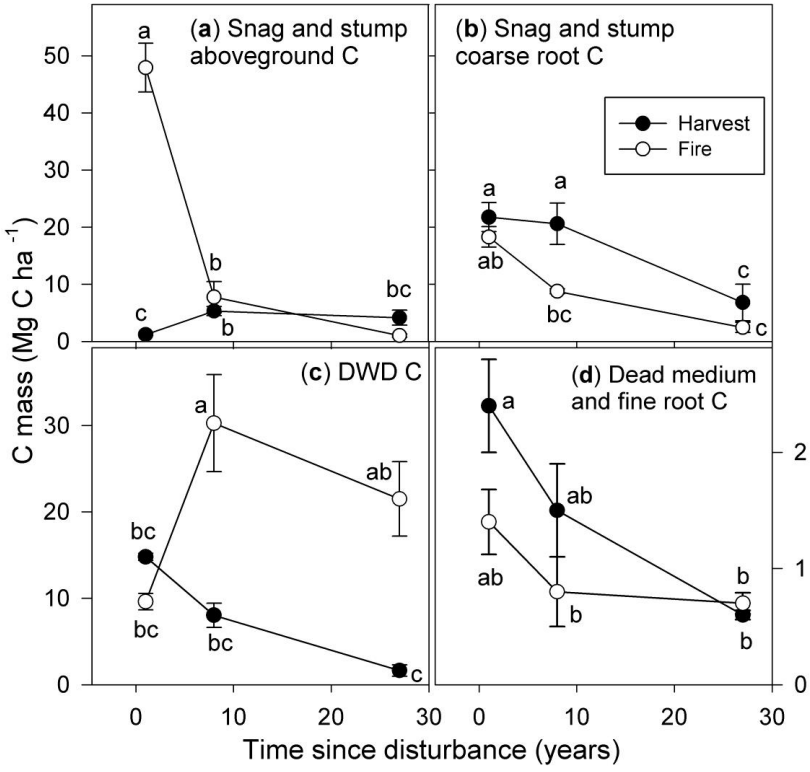
624 **Figure 4**



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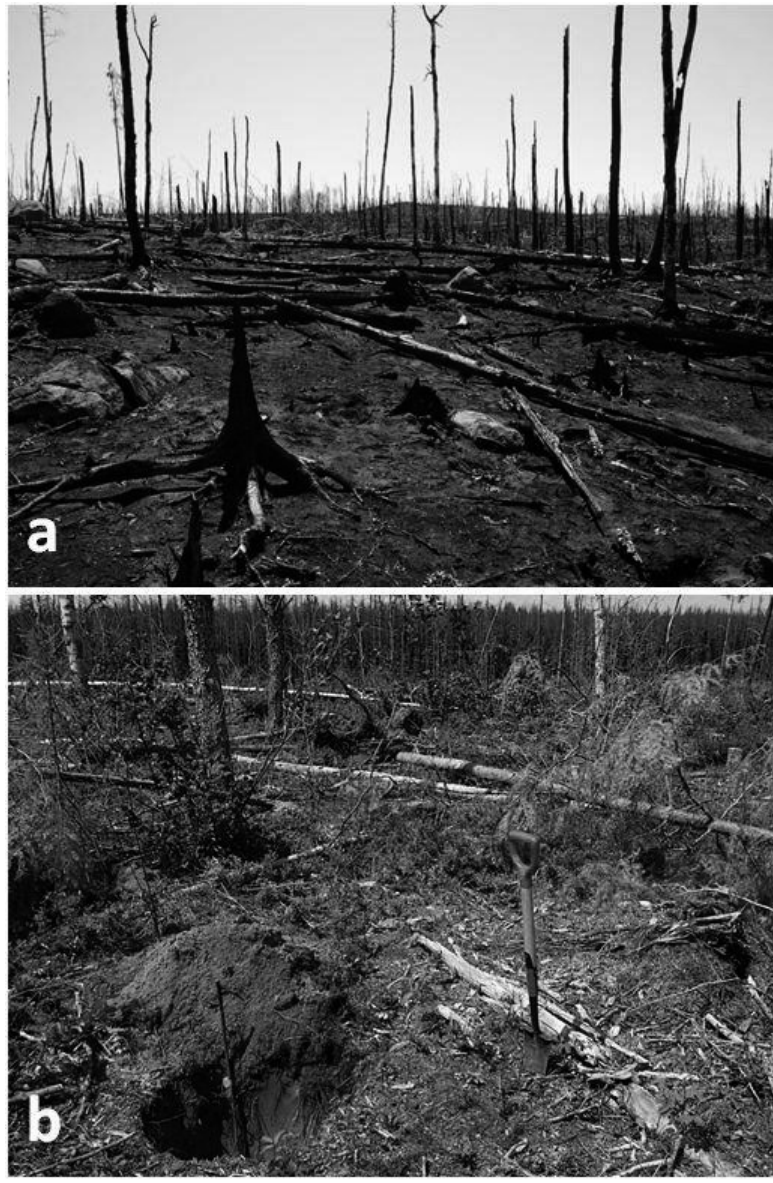
627 **Figure 5**



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LIST OF PUBLICATIONS

Indexed in ISI web of science

1. **Seedre, M.**, Taylor, A.R., Chen, H.Y.H. and Jõgiste, K. 2013. Dead wood density of five boreal tree species in relation to field assigned decay class. Forest Science 59(3):261–266.

2. **Seedre, M.**, Shrestha, B.M., Chen, H.Y.H., Colombo, S. and Jõgiste, K. 2011. Carbon dynamics of North American boreal forest after stand replacing wildfire and clearcut logging. Journal of Forest Research 16: 168–183.

3. **Seedre, M.** and Chen, H.Y.H. 2010. Carbon dynamics of aboveground live vegetation of boreal mixedwoods after wildfire and clearcutting. Canadian Journal of Forest Research 40: 1862–1869.

4. Lindbladh, M., Abrahamsson, M., **Seedre, M.** and Jonsell, M. 2007. Saproxylic beetles in artificially created high stumps of spruce and birch within and outside hotspot areas. Biodiversity and Conservation 16: 3213–322.

5. Köster, K., **Seedre, M.**, Tukia, H., Niklasson, M. and Jõgiste, K. 2004. Nature conservation and dead wood in forest ecosystems. Transactions of the Faculty of Forestry, Estonian Agricultural University 37: 13–16.

Other peer reviewed publications

6. Köster, K., **Seedre, M.**, Jõgiste, K. and Tukia H. 2003. Coarse woody debris analysis in Karula and Lahemaa National Park. Transactions of the Faculty of Forestry, Estonian Agricultural University, 36: 72–81.

7. **Seedre, M.**, Köster, K. ja Jõgiste, K. 2002. Metsaökosüsteemi looduslikkuse taastamine ja vastava katseala iseloomustus Lahemaa Rahvuspargis. Abstract: Forest ecosystem restoration and description of sample area in Lahemaa National Park. Transactions

of the Faculty of Forestry, Estonian Agricultural University, 35: 85–91.

In preparation

8. **Seedre, M.**, Taylor, A.R., Brassard, B.W., Chen, H.Y.H. and Jõgiste, K. (Manuscript). Total ecosystem carbon dynamics in young boreal forest: Comparison of wildfire and harvesting effects.

9. Taylor, A., **Seedre, M.**, Brassard, B.W., Chen, H.Y.H. (Manuscript). Post-fire recovery of ecosystem production over a 203-year succession gradient in the boreal forest.

10. Polyachenko, O., Vodde, F., Jõgiste, K., Shorohova, E., Köster, K., **Seedre, M.**, Metslaid, M. (Manuscript). Survival of canopy trees during and after wind disturbances in European conifer dominated boreal and hemi-boreal forests: a review.

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2005–2006 **MSc course "Master of European Forestry"**, University of Joensuu, Finland; Swedish University of Agricultural Sciences, Sweden; University of Natural Resources and Applied Life Sciences, Vienna Austria; University of Lleida, Spain; Wageningen University, The Netherlands; Albert-Ludwig University of Freiburg, Germany.

2004–2005 **MSc with major in Biology**, "Saproxylic beetles in artificially created high stumps of spruce and birch three years after cutting". Supervisor Prof. Matts Lindbladh. Swedish University of Agricultural Sciences.

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1999–2003 **Bachelor Degree in Forest Management**, "Coarse Woody Debris analysis in Karula and Lahemaa National Park". Supervisor Prof. Kalev Jõgiste. Estonian Agricultural University.

EXPERIENCE:

- Oral and poster presentations in scientific conferences;
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CV APPENDICES

PARTICIPATED COURSES:

1. "**Physics and chemistry of air pollution and their effects: field course and data analysis**". 21.–29.03.2011 Hyytiälä Forestry Field station, Southern Finland. 5 ECTS, University of Helsinki.

2. "**Global Climate Change; introductory course with the focus on palaeoecology**". 04.–07.04.2011 Tartu. Dr. Nadia Kettel-Solovieva. 2 EAP. Estonian University of Life Sciences.

3. "**Boreal Forest Stand Dynamics and Ecosystem Management of Eastern Canada**". 02.–05.05.2011 Umeå, Sweden. Prof. Yves Bergeron (Université du Quebec in Abitibi Témiscamingue and Université du Québec à Montréal) and Prof Francine Tremblay (Université du Québec en Abitibi-Témiscamingue), 2 ECTS, Swedish University of Agriculture Sciences.

4. "**Basis of the art of self-expression**" AU.159. 02.–04.12.2009, Estonian University of Life Sciences. Prof. Ingo Normet. 10 h.

5. "**Technical terminology and its use in science**" AU.283. 13.01.–01.02.2011, Estonian University of Life Sciences. Dr. Arvi Tavast. 2 EAP.

6. "**Media training**" AU.278 17.12.2010, Estonian University of Life Sciences, MSc Tiit Hennoste. 5 h.

7. "**Methods of active learning**" 26.–27.05.2011, Estonian University of Life Sciences, Piret Kärtner.

8. "**Carbon dynamics in terrestrial ecosystems with implications for climate change mitigation**". 12.–16.09.2011 Joensuu, Finland. University of Eastern Finland.

CONFERENCES PRESENTATIONS:

1. Oral presentation "**Carbon dynamics of aboveground live vegetation of boreal mixedwoods after wildfire and clearcutting**". First natural science doctoral student's conference seminar. 11.–12.05.2010, Võrumaa, Haanjamehe farm. Award winning presentation.

2. Oral presentation "**Carbon dynamics of aboveground live vegetation of boreal mixedwoods after wildfire and clearcutting**". "Adaptation of Trees and Stands to Forest Disturbances: Management Considerations" Conference hosted IX international workshop of SNS network Natural Disturbance Dynamics Analysis for Forest Ecosystem Management jointly together with European INTERREG IVC project FUTUREforest workshop. 18.–21.10.2010 International Conference in Riga Latvia.

3. Oral presentation "**Boreal forest carbon dynamics after wildfire and clearcutting**". Meeting of Estonian Naturalists´Society. 03.11.2010, Tartu.

4. Oral presentation "**Boreal forest carbon dynamics**". Young forestry scientist and practicians contact seminar.08.12.2010, Tallinn, RMK (State Forest Management Centre) headquarters.

5. Oral presentation "**Carbon dynamics of North American boreal forest after stand replacing wildfire and clearcut logging: a review**". Doctoral students conference "Next generation insights into geosciences and ecology".12.–13.05.2011, Tartu, Dorpat conference centre.

6. Oral presentation "**Total ecosystem carbon dynamics in young boreal forest: Comparison of wildfire and harvesting effects**". Forest biology group meeting.07.02.2013, Estonian University of Life Sciences, Tartu.

7. Oral presentation "**Total ecosystem carbon dynamics in young boreal forest: Comparison of wildfire and harvesting effects**". The 2nd Conference of Doctoral School of Earth Sciences and Ecology "Down to Earth". 16.–17.05.2013 Tallinn.

8. Oral presentation "**Total ecosystem carbon dynamics in young boreal forest: Comparison of wildfire and harvesting effects**". Fourth natural science doctoral student's conference seminar, 18.–19.05.2013 Voore.

9. Poster presentation "**Total ecosystem carbon dynamics in young boreal forest: Comparison of wildfire and harvesting effects**". 56th Symposium of the International Association for Vegetation Science (IAVS 2013). 26.–30.06.2013 Tartu.

TEACHING:

1. Forest ecology practical lessons:
    a. Forest biodiversity, 27.10.2010;
    b. Light and forest trees, 03.11.2010.

2. Course: "Boreal fauna, flora, communities and ecosystems"
    BioLandMan Erasmus course. PK.1120, 6h of teaching, 1EAP. 11.–13.04.2011.

3. Co-supervision (with Kristi Teppo) of Katrin Seglinš bachelor thesis "Carbon dynamics in boreal forest ecosystem", grade B.

POPULAR SCIENCE ARTICLES:

1. "**Green dilemma: who is the real climate hero**" (In Estonian, "Roheline dilemma: kes on tõeline kliimakangelane?"). Novaator, Delfi Forte (23.02.2011), Maaleht (02.04.2011).

2. "**Space for time substitution**" (In Estonian, "Aja asendamine ruumiga"). Doctoral School of Earth Sciences and Ecology 2009–2015 journal. April 2013.

3. Media coverage of doctoral thesis by Marju Himma "**The use of wood saves the environment**" (In Estonian, "Puidu kasutamine säästab keskkonda"). Tartu Postimees (04.06.2013).

ELULOOKIRJELDUS

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Rahvus: Eestlane

HARIDUS:

2009–2013 **Eesti Maaülikooli doktorant**, töö teema "Häiringurežiimi mõju metsaökosüsteemi süsinikuvoogudele". Juhendaja Prof. Kalev Jõgiste, kaasjuhendaja Prof. Han Y.H. Chen.

2006–2009 **Magistrikraad metsanduses, doktoritöö planeerimine ja andmete kogumine**, töö teema "Kesk-Kanada boreaalse segametsa süsinikudünaamika". Juhendaja Prof. Han Y.H. Chen. Lakehead University, Kanada.

2005–2006 **Magistrikursus "Euroopa metsanduse magister"**, University of Joensuu, Soome; Swedish University of Agricultural Sciences, Rootsi; University of Natural Resources and Applied Life Sciences, Austria; University of Lleida, Hispaania; Wageningen University, Holland; Albert-Ludwig University of Freiburg, Saksamaa.

2004–2005 **Magistrikraad bioloogias**, töö teema „Puiduüraskid kuuse ja kase kõrgetel tehiskändudel kolm aastat peale raiet". Juhendaja Prof. Matts Lindbladh. Swedish University of Agricultural Sciences.

2003–2004 **Magistrikursus „Läänemere ümbruse säästlik metsandus"** (tänaseks „Euroforester"), Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences.

1999–2003 **Bakalaureuse kraad metsamajanduse erialal**, töö teema „Lagupuidu analüüs Lahemaa ja Karula rahvuspargis". Juhendaja Prof. Kalev Jõgiste. Eesti Põllumajandusülikool.

KOGEMUSED:

- Suulised- ja posterettekanded teaduskonverentsidel;
- Loengute andmine ja bakalaureusetöö juhendamine;
- Mahukad välitööd Eestis, Rootsis ja Kanadas;
- Teadusartiklite ja projektitaotluste kirjutamine.

ARVUTIKASUTUS: Windows, Macintosh ja Linux operatsioonisüsteemid, Microsoft Office tarkvara, Apple'i peamised programmid, Photoshop, SigmaPlot, statistiline tarkvara SPSS, Minitab ja R.

KEELTEOSKUS:

- Eesti: Emakeel;
- Inglise: Väga hea;
- Prantsuse: Algaja;
- Vene: Keskmine;
- Saksa: Keskmine.

HUVID: Teadus, muusika, õlle pruulimine, kokandus, fotograafia, kunst, kitarrimäng, loodus, filosoofia, reisimine, lumelauasõit.

ELULOOKIRJELDUSE LISAD

OSALETUD KURSUSED:

1. "**Physics and chemistry of air pollution and their effects: field course and data analysis**". 21.–29.03.2011 Hyytiälä Forestry Field station, Lõuna Soome. 5 ECTS, University of Helsinki.

2. "**Global Climate Change; introductory course with the focus on palaeoecology**". 04.–07.04.2011 Tartu. Dr. Nadia Kettel-Solovieva. 2 EAP. Maaülikool.

3. "**Boreal Forest Stand Dynamics and Ecosystem Management of Eastern Canada**". 02.–05.05.2011 Umeå, Rootsi. Prof. Yves Bergeron (Université du Quebec in Abitibi Témiscamingue ja Université du Québec à Montréal) ja Prof Francine Tremblay (Université du Québec en Abitibi-Témiscamingue), 2 ECTS, Swedish University of Agriculture Sciences.

4. "**Eneseväljenduskunsti alused**" AU.159. 02.–04.12.2009, Maaülikool. Prof. Ingo Normet. 10 h.

5. "**Oskuskeel ja selle rakendatavus teaduses**" AU.283. 13.01.–01.02.2011, Maaülikool. Dr. Arvi Tavast. 2 EAP.

6. "**Meediakoolitus**" AU.278 17.12.2010, Maaülikool, MSc Tiit Hennoste. 5 h.

7. "**Aktiivõppe meetodid**" 26-–27.05.2011, Maaülikool, Piret Kärtner.

8. "**Carbon dynamics in terrestrial ecosystems with implications for climate change mitigation**". 12.–16.09.2011 Joensuu, Soome. University of Eastern Finland.

KONVERENTSIETTEKANDED:

Suulised ettekanded

1. "**Boreaalse segametsa elus taimestiku maapealse osa süsinikudünaamika peale põlengut ja lageraiet**". Esimene loodusteaduste doktorandide konverents-seminar. 11.–12.05.2010, Võrumaa, Haanjamehe talu. Auhinnatud ettekanne.

2. "**Carbon dynamics of aboveground live vegetation of boreal mixedwoods after wildfire and clearcutting**". "Adaptation of Trees and Stands to Forest Disturbances: Management Considerations" Conference hosted IX international workshop of SNS network Natural Disturbance Dynamics Analysis for Forest Ecosystem Management jointly together with European INTERREG IVC project FUTUREforest workshop. 18.–21.10.2010, Rahvusvaheline konverents, Riia, Läti.

3. „**Boreaalse segametsa süsinikudünaamika peale põlengut ja lageraiet**" Eesti Loodusuurijate Seltsi metsandussektsiooni koosolek. 03.11.2010, Metsamaja, Tartu.

4. **"Süsinikudünaamika boreaalses metsa-ökosüsteemis"**. Metsanduse noorteadlaste ja praktikute kontakt-seminar RMK's. 08.12.2010, Tallinn, RMK peamaja.

5. "**Carbon dynamics of North American boreal forest after stand replacing wildfire and clearcut logging: a review**". Rahvusvaheline doktorantide konverents "Next generation insights into geosciences and ecology".1 12.–13.05.2011, Tartu, Dorpat'i konverentsikeskus.

6. "**Total ecosystem carbon dynamics in young boreal forest: Comparison of wildfire and harvesting effects**". Metsabioloogia osakonna koosolek. 07.02.2013, Maaülikool, Tartu.

7. "**Total ecosystem carbon dynamics in young boreal forest: Comparison of wildfire and harvesting effects**". Rahvusvaheline konverents The 2nd Conference of Doctoral School of Earth Sciences and Ecology "Down to Earth". 16.–17.05.2013 Tallinn.

8. "**Kogu ökosüsteemi süsiniku dünaamika noores boreaalses metsas, võrdlus metsatulekahju ja lageraie vahel**". Neljas loodusteaduste doktorantide konverents-seminar, 18.–19.05.2013 Voore.

Posterettekanne

1. "**Total ecosystem carbon dynamics in young boreal forest: Comparison of wildfire and harvesting effects**". 56th Symposium of the International Association for Vegetation Science (IAVS 2013). 26.–30.06.2013 Tartu.

ÕPETAMINE:

1. Metsaökoloogia praktikumid:
    a. Metsade bioloogiline mitmekesisus, 27.10.2010;
    b. Puuliikide valusnõudlikkus ja varjutaluvus, summaarse radiatsiooni jagunemine metsas, 03.11.2010.

2. Kursus: "Boreal fauna, flora, communities and ecosystems" BioLandMan Erasmuse kursus. PK.1120, 6h, 1EAP. 11.–13.04.2011.

3. Katrin Seglinš'i bakalaureusetöö kaasjuhendamine koos Kristi Teppoga. Teema „Süsinikudünaamika boreaalses metsaökosüsteemis", kaitstud hindele B.

POPULAARTEADUSLIKUD ARTIKLID:

1. "**Roheline dilemma: kes on tõeline kliimakangelane?**". Novaator, Delfi Forte (23.02.2011), Maaleht (02.04.2011).

2. "**Aja asendamine ruumiga**". Maateaduste ja Ökoloogia Doktorikooli ajakiri. Aprill 2013.

3. Doktoritööd kajastav artikkel, Marju Himma "**Puidu kasutamine säästab keskkonda**". Tartu Postimees (04.06.2013).

VIIS VIIMAST KAITSMIST

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GENETIC DIVERSITY, GENOTYPIC STRUCTURE AND VULNERABILITY OF NATIVE POPULATIONS OF SICKLE MEDIC (*MEDICAGO SATIVA* SSP. *FALCATA*) IN ESTONIA
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